Year: 2018

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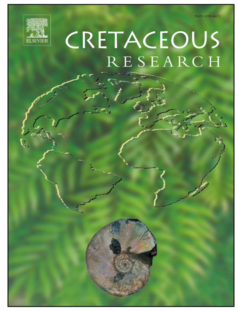
DOI: https://doi.org/10.1016/j.cretres.2017.09.021

Originally published at:
Guinot, Guillaume; Carrillo-Briceño, Jorge (2018). Lamniform sharks from the Cenomanian (Upper Cretaceous) of Venezuela. Cretaceous research, 82:1-20.
DOI: https://doi.org/10.1016/j.cretres.2017.09.021

Accepted Manuscript



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PII: S0195-6671(17)30297-5

DOI: 10.1016/j.cretres.2017.09.021

Reference: YCRES 3720

To appear in: *Cretaceous Research*

Received Date: 19 June 2017

Revised Date: 4 September 2017

Accepted Date: 23 September 2017

Lamniform sharks from the Cenomanian (Upper Cretaceous) of Venezuela

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Abstract. Sampling of Cenomanian fossil-rich horizons within the La Luna Formation of two localities in the Zulia and Trujillo states (northern Venezuela) yielded numerous shark teeth belonging to various species within the order Lamniformes (Mackerel sharks). Twelve lamniform species were identified including three new species (*Squalicorax lalunaensis* sp. nov., *Squalicorax moodyi* sp. nov., *Acutalamna karsteni* gen. et sp. nov.) and the genus *Microcarcharias* gen. nov. is proposed to accommodate with the peculiar morphology of the small-sized odontaspidid *M. saskatchewanensis*. Other taxa reported here include *Cretoxyrhina mantelli*, *Cretolamna* sp., cf. *Nanocorax* sp. and five *Squalicorax* species left in open nomenclature. This is the first report of chondrichthyans from the mid-Cretaceous of Venezuela and one of the few records of this group from the Cenomanian of South America. The composition of these assemblages suggests some degree of endemism in the La Luna Sea but also possible connexions with the Western Interior Seaway. One of the most striking features of these assemblages is the high anacoracid diversity (eight species) despite the corresponding outer shelf/upper slope palaeoenvironments of the La Luna Formation. The high diversity of these opportunistic predators is probably related to the high diversity of medium to large marine vertebrates that provided food resources.

Keywords. Chondrichthyes; Anacoracidae; La Luna Formation; South America; Upper Cretaceous.

1. Introduction

Mackerel sharks (Lamniformes) form a clade of mainly marine selachians represented today by fifteen species included within ten genera (Weigmann, 2016). Despite their relative low diversity, recent lamniforms display a wide range of marine habitats (from intertidal to bathypelagic zones), a large array of behaviours (slow-swimming benthopelagic to fast oceanic swimmers) and include a number of feeding strategies (top predators, filter feeders, opportunistic predators, scavengers). Analysis of the fossil record indicates that lamniform diversity was much higher in the past, especially in the Cretaceous-Paleogene interval (Cappetta, 2012; Guinot and Cavin, 2016). This, along with the large range of morphological disparity (Compagno, 1990) and body size (1 to 10 meters) of modern representatives of this clade suggest that Recent Mackerel sharks gather derived relic forms of a formerly flourishing group. One of the key events in the lamniform evolutionary history is their dramatic mid-Cretaceous (~125 - 90 Ma) diversification (Cappetta, 2012; Guinot et al., 2012; Guinot and Cavin, 2016; Underwood, 2006) that occurred relatively early after the first appearance of the group in the fossil record (Valanginian, Rees, 2005). This marked Aptian-Cenomanian radiation resulted in the rapid apparition of a number of modern and fossil lamniform clades showing a variety of specialisations and ecological characteristics. These include small nectobenthic predators that were comparable in size range, dental morphology, ecology and even gross general morphology with some modern Ground Sharks (Carcharhiniformes) (Siverson et al., 2007; Vullo et al., 2016). Following this mid-Cretaceous diversification, lamniforms became a major component of chondrichthyan faunas throughout the Late Cretaceous-Paleogene interval. The abundance and diversity of lamniform taxa since their mid-Cretaceous diversification suggest that their generic diversity is relatively well known in comparison to other chondrichthyan groups (Underwood et al., 2016). However, the Cretaceous lamniform species diversity remains difficult to assess due to poor definition/illustration of many nominal species and difficulties in assessing intraspecific morphological variations (Siverson et al., 2007; Siversson et al., 2015). A more general issue is that our perception of Cretaceous chondrichthyan diversity is mainly based on European, North African and North American localities, whereas data from the southern hemisphere and particularly from South America is comparatively scarce.

The mid-Cretaceous chondrichthyan record in South America is based on a few isolated reports. In Brazil, the upper Aptian–lower Albian Santana Formation of the Araripe Basin yielded several articulated specimens of the batomorphs *Iansan beurleni* (Silva Santos, 1968) and *Stahlraja sertanensis* Brito, Leal and Gallo, 2013 and of the hybodont *Tribodus limae* Brito and Ferreira, 1989. Isolated rostral denticles of the sclerorhynchiform *Atlanticopristis equatorialis* Pereira and Medeiros, 2008 were reported from the lower Cenomanian Alcântara Fm. The Peruvian record is restricted to the lamniform species *Priscusurus adruptodontus* Kriwet, 2006 from the Albian of northwestern Peru. Turonian chondrichthyans include *Ptychodus chappelli* Reinhart, 1951 (probably synonymous with *P. mammilaris* Agassiz, 1838, see Cappetta, 2006) and *Onchosaurus* species from Colombia (Parámo Fonseca, 1997), also reported from Ecuador (Dunkle, 1951). Fossil record of mid-Cretaceous chondrichthyans from Venezuela is no richer than elsewhere in South America and is restricted to the Cenomanian-Campanian of La Luna Formation. These reports include *Ptychodus atcoensis* Hamm, 2009, probably from the Coniacian (Carrillo-Briceño and Lucas, 2013), "*Ptychodus decurrens*" Agassiz, 1835 from the Cenomanian-Santonian (Carrillo-Briceño, 2009) and *Ptychodus cyclodontis* Mutter, Iturralde-Vinent and Carmona, 2005 reported as *Ptychodus* sp. from the Cenomanian-Santonian of La Luna Fm. (Carrillo-Briceño, 2009) and from an unknown locality (Venezuela or Colombia) tentatively assigned to La Luna Fm. (Brito and Janvier, 2002). Moody and Maisey (1994) signaled the presence of *Squalicorax* in the Cenomanian of La Luna Quarry but did not provide illustrations. The presence of *Squalicorax* from La Luna Quarry represents the only report of non-ptychodontid chondrichthyans from the mid-Cretaceous of Venezuela (Cenomanian of La Luna Fm.) and one of the two records of Cretaceous lamniforms from this region along with the Maastrichtian record of *Serratolamna serrata* from the Andes region (Carrillo-Briceño et al., 2008). Based on the fossil shark specimens of Moody and Maisey (1994) from the La Luna Quarry (Sierra de Perijá, Zulia state) and additional collected material from the Cordillera de Mérida (Trujillo state), this paper provides the first description of lamniform sharks from the Cenomanian of Venezuela and adds to the knowledge of the mid-Cretaceous marine diversity in the northernmost part of South America.

2. Geographical and geological Settings

The specimens described here come from two different quarry outcrops in western Venezuela (Fig. 1), where rocks of La Luna Formation are extracted for cement production. One of the locations is the quarry exploited by Cementos Andinos company and located in the Andes range (Cordillera de Mérida), east of Lake Maracaibo, 10 km to the northeast of Monay city (9° 36.57' 06" N, 70° 24' 14" W), Candelaria Municipality, Trujillo estate (Chejendé region, Figure 2). The second outcrop is located in La Luna Quarry, Sierra de Perijá, west of Maracaibo Lake, approximately 20 km to the northwest of Villa del Rosario town (10° 22' 21" N, 72° 27' 45" W), Rosario de Perijá Municipality, Zulia estate (Maracaibo Basin, Fig. 2).

La Luna Formation (Upper Cretaceous) is characterized by a sequence of marine rocks deposited under anoxic-dysoxic conditions along the passive margin of northern South America during the Cenomanian-Campanian (Zapata et al., 2003) and is the most prolific petroleum source rock in western Venezuela and part of eastern Colombia (Tribovillard et al., 1991; Zapata et al., 2003; Zumberge, 1984). La Luna Formation is characterized by alternating black or dark-gray limestones and organic calcareous shales, where calcareous concretions are abundant (Davis et al., 1999; Juana et al., 1980; Tribovillard et al., 1991) and reaching in some cases very large sizes (e.g. Albino et al. 2016, fig. 3). The unit has been subdivided by Renz (1959) into three members exposed in the southeast of the Maracaibo basin (Lara and Trujillo states, Cordillera de Mérida): the lower, La Aguada Member (~ 60 m thick of a dense dark-grey limestones and black shales); the middle, Chejendé Member (~ 80 m thick of black shales and marls); and the upper, Timbetes Member (~ 90 m thick of laminated limestones and shales).

The fossiliferous outcrop of the Cementos Andinos Quarry belongs to the Aguada Member (Fig. 2) and is characterized by dense dark-grey limestones of up to ~ 60-70 cm thick, intercalated with compact and laminated black/dark-grey shales. The material reported here was collected from successive black shale horizons in association with ichnofossils, molluscs (bivalves, gastropods and cephalopods), bony fishes (Carrillo-Briceño et al., 2012) and marine squamate remains (Albino et al., 2016). For more details about the stratigraphy of the Cementos Andinos Quarry see Albino et al. (2016).

Specimens from La Luna Quarry were collected from organic calcareous layers made of thin alternations of compact and light brown siliceous-rich platy limestones and darker shales in the lowest part of the exposed section in the La Luna Formation, just above the contact with the underlying Maraca Formation of the Cogollo Group (Moody and Maisey, 1994, p. 2). Shark teeth were found in association with abundant and mostly disarticulated bony fish remains. A preliminary report on fossil fishes from the La Luna Quarry was made by Moody and Maisey (1994) who mentioned one shark taxon (*Squalicorax* sp.) and various osteichthyans (enchodontids, *Belonostomus*, *Bananogmius* and unidentified teleost scales and bones). A Cenomanian age was proposed for rocks of La Luna Formation overlaying the Maraca Formation in the Maracaibo Basin (e.g. Juana et al., 1980, fig. IV-12; Dot et al., 2015, fig. 4). However, other authors (Renz, 1982, fig. 4; Erlich et al., 1999, figs. 3-4) suggested the existence of a regional hiatus in the Sierra de Perijá at the base of La Luna Formation where most of the Cenomanian is lacking. Considering the Sierra de Perijá section suggested by Erlich et al. (1999), the basal section of La Luna Formation in La Luna Quarry could correspond to a late Cenomanian age.

3. Material and Methods

Specimens from La Luna Quarry were surface-collected in the 90s by paleontologist John M. Moody and other members and collaborators of the Museo de Biología de La Universidad del Zulia

Maracaibo, Zulia estate. Surface-collected specimens were extracted from the sediment both chemically (3% formic acid) and mechanically. About 2 Kg of rock were subsequently bulk-collected by one of us (JDCB.) from the fossil-rich horizon, processed in 7.5% formic acid and sieved down to 300 μm mesh. This yielded abundant disarticulated osteichthyan microremains but no chondrichthyans. Selachian specimens are well preserved and show no signs of abrasion but nearly all specimens are weakly fractured.

Specimens from Cementos Andinos Quarry were surface-collected (between 2013 and 2016) by one of us (JDCB) with the collaboration of the personal of this institution. All specimens are heavily fractured due to strong sediment compaction and some teeth show weak degree of abrasion. Surface-collected specimens were extracted from the sediment both chemically (3% formic acid) and mechanically. About 3 Kg of rock were processed in 7.5% formic acid and sieved down to 300 μm mesh. This yielded some small selachian and osteichthyan tooth fragments and distorted osteichthyan vertebrae.

Specimens from Zulia state (La Luna Quarry) are housed in the collections of the Museo de Biología de La Universidad del Zulia Maracaibo, Zulia estate (with the acronym MBLUZ-P) and specimens from Trujillo state (Cementos Andinos Quarry) are housed in the paleontological collection of the Alcaldía Bolivariana de Urumaco, Venezuela (with the acronym AMU-CURS).

4. Systematic Palaeontology

The terminology and systematic framework used here largely follow those of Cappetta (2012).

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Cohort Euselachii Hay, 1902

Subcohort Neoselachii Compagno, 1977

Order Lamniformes Berg, 1958

Family Anacoracidae Casier, 1947

Genus *Nanocorax* Cappetta, 2012

cf. *Nanocorax* sp.

Figures 3A-B

Material. One tooth (AMU-CURS-906) from Cementos Andinos quarry (Trujillo state).

Description. This small-sized tooth is slightly higher (5.5 mm) than wide (4.5 mm) and occupies an anterolateral jaw position. The main cusp is bent to the posterior, thin and elongate. The lingual face of the main cusp is convex while the labial face is flat with the exception of a light median bulge at the base of the crown. The mesial cutting edge is slightly concave whereas the distal one is straight. A low mesial heel is present, poorly individualised from the main cusp and oblique. The distal heel is nearly horizontal. Both mesial and distal heels have abrupt and vertical lateral edges. The cutting edges are smooth and continuous from the apex of the main cusp until the lateral edges of the heels. A rather well-developed lingual neck marks the limit between the crown and root. The root is high and stubby with short, thick and basally-oriented lobes. The distal root lobe is more developed and narrower than the distal one. The labial root face exhibits a very slight bulge that overhangs a depressed median region where several large foramina open. A central and two additional foramina are present on the basal root face.

Remarks. The morphology of this tooth including nearly flat labial face, smooth cutting edges and heels, stubby root with short lobes is rather uncommon among anacoracid species. The root – and to a lesser extent the crown – morphologies bear resemblances with those of some *Nanocorax* teeth, in particular lateral teeth of *Nanocorax crassus* (Cappetta and Case, 1999) from the upper Cenomanian Woodbine Formation of Texas (Cappetta and Case, 1999, 1975; Welton and Farish, 1993). However, lateral teeth of *N. crassus* have a more convex labial crown face, more lingually oriented main cusp, less differentiated mesial heel and more developed mesial cutting edge. *Nanocorax microserratodon* (Shimada, 2008) described from the ?Coniacian of Kansas and also known from the Santonian to Campanian of England, France, Belgium and Morocco (see Guinot et al., 2013) is the other nominal *Nanocorax* species known so far. Teeth of *N. microserratodon* differ from the Venezuelan tooth in having a wider main cusp with a typical mesiodistal twisting, small serrations unevenly present on main cusp and heels, more labio-lingually developed crown and root, weak demarcation between main cusp and mesial heel and stronger labial crown bulge. More material is needed to better assess the systematic attribution of the Venezuelan specimen, especially considering the heterodonty of some *Nanocorax* species.

Genus *Squalicorax* Whitley, 1939

Squalicorax moodyi sp. nov.

Figures 3C-H

Derivation of name. The species is named in honour of John M. Moody, who left a valuable legacy in the study of Mesozoic vertebrate faunas from Venezuela.

Holotype. MBLUZ P-432-C.

Material. Four teeth (MBLUZ P-430, MBLUZ P-432-C, MBLUZ P-432-D and MBLUZ P-881-B) from La Luna quarry (Zulia state).

Type stratum. Organic calcareous limestone/shales in the lowest part of the La Luna Formation, just above the contact with the underlying Maraca Formation of the Cogollo Group (see Moody and Maisey, 1994).

Diagnosis. Anacoracid shark with small teeth not exceeding 8 mm in both width and height. Gradient monognathic heterodonty. Main cusp triangular, rather wide and inclined distally; strongly convex lingual crown face; wide lingual neck. No differentiated mesial heel. Distal heel low, convex and oblique. Apex of main cusp occasionally extends slightly beyond the distal edge of the heel. Cutting edges and heels serrated; serrations taper near apex and lateral extremities of heels. Basal edge of labial crown face, scalloped, strongly concave with marked bulge. Root lobes well developed, separated by deep concavity of basal root edge. Mesial root lobe thin with sharp extremity; distal lobe wider with rounded extremity. Concave mesial and distal root edges.

Description. Teeth of anteriormost position are slightly higher (8 mm) than wide (6 mm), strongly mesio-distally compressed and asymmetrical. The triangular main cusp is high and bent distally with a strongly convex labial face and a flat labial face. The apex of the main cusp is sharp and slightly bent labially. The mesial cutting edge of the main cusp is convex and connect to a very low, poorly individualized and strongly oblique mesial heel. The distal cutting edge of the main cusp is slightly concave in its median region and is separated from the distal heel by a notch. The distal heel is rather low, convex and moderately oblique. The lateral extremities of both the mesial and distal heels terminate in a thin enamelled blade that is supported by a narrow root protuberance and oriented labially. A broad lingual neck is present in the basal region of the crown. The basal edge of the labial crown face exhibits a strong triangular concavity in its median region with a marked bulge that overhangs the root. Root foramina pierce the enamelled bulge, which confers a scalloped aspect to the bulge. The labial marginal areas of the basal crown face are flat but oriented labially, whereas the labial face of the main cusp is vertical. The cutting edges and heels have small and rather regular serration that diminish in size and tapper toward the lateral edge of the heels and near the apex of the main cusp. The root is bilobate and mesio-distally compressed. The root lobes are well-developed and separated by a deep and wide concavity of the basal root edge. The lingual root face exhibits a wide and poorly individualized lingual protuberance that is pierced by a wide nutritive foramen along with other smaller foramina. Additional rather wide foramina are present on the basal root face of the lobe. The mesial root lobe is thin with a relatively acute extremity whereas the distal lobe is much wider with a rounded labial edge. Both the mesial and distal edges of the root are markedly concave in lingual view. The labial root face is low and bears a marked concavity in it central area. Large, oval-shaped foramina open near (in lateral regions) or on (in medial region) the crown/root edge. Teeth from more lateral positions become gradually wider than high with a strongly distally bent main cusp than can extend slightly beyond the distal edge of the heel. The mesial heel is not differentiated from the cutting edge of the main cusp whereas the distal heel is similar in shape to that of anterior teeth but less inclined to the base of the tooth. The mesial cutting edge is slightly convex whereas the distal on is nearly straight. The shape of the apex varies in teeth from anterolateral and lateral positions, being either bent to the commissure or erect, but in all teeth show some degree of labial inclination. The labial concavity of the basal crown edge is wider and less deep than in anterior teeth. The root is mesio-distally elongate with a flat basal face and a wider concavity of the basal root edge than in anterior teeth.

Remarks. By the morphology of their asymmetrical root lobes, wide and deep concavity of basal root edge, broad neck, labially inclined apex, regular serrations and strongly convex labial crown face, teeth of *Squalicorax moodyi* sp. nov. differ from those of other known mid-Cretaceous anacoracid species. Several nominal and unnamed small-sized anacoracid species are known from mid-Cretaceous deposits. The species *Squalicorax volgensis* (Glikman in Glikman and Shvazhaite, 1971) was described from the lower Cenomanian of Saratov Province (Russia) based on scarce and incomplete specimens but additional material from the type stratum was figured by Siverson et al. (2007). Teeth of this species differ from those of *Squalicorax moodyi* sp. nov. by the absence of serrations, more squared distal root lobe in basal view, absence of marked notches on the mesial and distal edges of the root and more marked notch between the main cusp and distal heel. *Squalicorax pawpawensis* Siverson, Lindgren and Kelley, 2007 is another mid-Cretaceous anacoracid with small-sized teeth known from the Albian of Texas. *Squalicorax pawpawensis* can be readily differentiated from the Venezuelan species by its lower rooted-teeth, more symmetrical root lobes, more irregularly present serrations, less deep concavity of basal root edge, more mesio-distally elongate root, absence of serration on distal heel and presence of small short vertical folds on basal edge of the labial crown face. Siverson (1996; p. 845, pl. 6) described specimens from the upper Cenomanian–lower Turonian Beedagong Claystone of Western Australia (now referred to as Haycock Marl) he attributed to *S. volgensis* but were later considered as a separated, unnamed species (Siverson et al., 2007). This taxon is probably conspecific or closely-related with the tooth reported as *S. volgensis* from the upper Cenomanian of Kansas (Shimada and Martin, 2008) and with some of the material published as *S. volgensis* by Cappetta and Case (1999; pl. 5, fig. 1) from the Turonian/Coniacian boundary of Texas, whereas the remaining of the specimens attributed to *S. volgensis* by Cappetta and Case (1999; pl. 4, figs. 7-8) from the Albian of Texas likely belong to *S. pawpawensis* (see Siverson et al., 2007). This unnamed taxon from Australia and USA differs from *Squalicorax moodyi* sp. nov. by its incipient serration occasionally present on the median region of the mesial cutting edge, higher and smooth distal heel, narrower neck and less marked – or absence of – notches on the mesial and distal edges of the root. Teeth of *Squalicorax priscoserratus* Siverson, Lindgren and Kelley, 2007 from the upper Albian Pawpaw Formation in Texas differ from *Squalicorax moodyi* sp. nov. in having a more gracile and narrower main cusp with more marked and coarser serrations, more mesio-distally elongate and lower root and less marked concavity of the basal root edge. A specimen figured by Glikman and Shvazhaite (1971; pl. 1, fig. 10 non figs. 8-9) from the Cenomanian of Russia (Saratov Province) as *Palaeoanacorax obliquus* (Reuss, 1845) represents a *Squalicorax* tooth from an anterior position in labial view. Although the species *S. obliquus* is based on a few poorly preserved teeth (Reuss, 1845; pl. 4, figs. 1-3) (see below), the specimen from Russia strongly differs from the type material collected from Turonian of Czech Republic. The general morphology of the Russian specimen could, however, fall within the variation of *Squalicorax moodyi* sp. nov. but the lack of additional view and poor quality of the line-drawing preclude further taxonomic assignment. Welton and Farish (1993; p. 120) figured an anterolateral and a posterior tooth of a *Squalicorax* sp. from the Weno Formation (Albian) of Texas. Teeth of this unnamed species are comparable is size and general morphology to *Squalicorax moodyi* sp. nov. suggesting that these two taxon are closely-related. However, the Albian taxon displays morphological differences including more symmetrical root with less developed distal lobe, less regular and irregularly present serrations, marked notch between main cusp and distal heel, and presence of vertical folds below the lingual neck, that differ from the species described here. To date, *Squalicorax moodyi* sp. nov. is only known from the type locality.

Squalicorax lalunaensis sp. nov.

Figure 4

Derivation of name. After the La Luna Formation.

Holotype. AMU-CURS-897.

Material. Twelve teeth (AMU-CURS-894 to 905) from Cementos Andinos quarry (Trujillo state).

Type stratum. Laminated black/dark-grey shales in the basal part of the La Aguada Member, La Luna Formation.

Diagnosis. Anacoracid shark with small teeth (less than 9 mm high) showing moderate degree of gradient monognathic and possibly dignathic heterodonty. Main cusp biconvex and triangular with narrow apical region; main cusp moderately to strongly inclined to the commissure with convex mesial cutting edge. Mesial heel elongate and well separated from main cusp in lateral teeth. Distal heel convex and individualized from main cusp by marked notch. Moderately developed basal bulge at base of labial crown face; basal bulge restricted to median region of crown in anteriors and laterals, extended to marginal crown edges in posteriors. Cutting edges of heels and main cusp sharp and well developed, devoid of serrations. Lingual neck of moderate and sub-equal width from mesial to distal edges. Root bilobate; mesial root lobe thin and elongate; distal lobe short with blunt extremity, nearly squared in laterals and posteriors. Lingual root face short and convex in profile view. Marginal edges of root concave in labial/lingual views. Basal root face flat except in anteriors. Labial root face with foramina of variable shape below basal crown bulge.

Description. Teeth of this species are relatively small, not exceeding 9 mm, and show a moderate degree of gradient monognathic and possibly dignathic heterodonty. Anterior teeth are higher than wide with a biconvex main cusp inclined to the commissure and sigmoid in lingual/labial views. The cutting edges of the main cusp and heels are sharp and rather developed. The mesial cutting edge of the main cusp is convex whereas the distal cutting edge is straight to slightly convex. The mesial heel is fairly low, short, oblique and separated from the main cusp by a slight concavity. The distal heel is convex and short, individualized from the main cusp by a notch. A moderately developed basal bulge is present at the base of the labial crown face but restricted to the median region of the crown, where it overhangs the root in occlusal view. The lingual crown face exhibits a neck of even width from its distal to medial extremities. The root is bilobate with labially oriented lobes separated by a V-shaped basal edge of variable depth and width according to tooth position. The mesial root lobe tend to be thinner and more elongate than the distal one that is short with a blunt extremity. The central areas of the basal root face is concave in profile view and bears a narrow and poorly marked lingual protuberance in anteriormost teeth where a central foramina is present. Other rather large foramina are present on the basal face of the lobes. The lingual face is fairly low and convex in profile view. A short vertical protuberance is present on the lingual face, below the lateral edge of the distal heel, which confers a concave outline of the distal root edge. The labial root face is flat in its marginal areas and concave in its center where several foramina of variable sizes are present immediately below the labial protuberance of the crown. Lateral teeth are wider than high and labio-lingually compressed with a strongly distally bent and sigmoid (in lingual view) main cusp. The mesial crown heel is high and elongate. The distal heel is well developed, sub-horizontal and separated from the main cusp by a deep notch. The basal bulge of the labial crown face is thin with an indented basal edge. The root is mesio-distally expanded with a flat basal face in profile view and concave mesial and distal edges in lingual/labial views. Posterior teeth have a sub-horizontal and sigmoid main cusp and vary from wider than high to as high as wide. The basal bulge of the labial crown face reaches the lateral margins of the crown. The distal root lobe has a nearly squared distal angle whereas the mesial one is sharp. Short vertical ridges are irregularly present on the labial bulge, below the distal heel. All teeth have smooth and sharp cutting edges.

Remarks. Teeth of *Squalicorax lalunaensis* sp. nov. differ from those of other anacoracid species by the combination of smooth and sharp cutting edges, sigmoid main cusp in labial-lingual view, distal heel separated from main cusp by marked notch, well-developed mesial heel in antero-laterals and laterals, bilobate and asymmetrical root with mesial root lobe thin and elongate and distal lobe short with blunt extremity (nearly squared in laterals and posteriors), and presence of short vertical folds on the labial crown face (below the distal heel). The morphology of posterior teeth (some rather large ones are mesio-distally short whereas other smaller ones are strongly mesio-distally elongate are morphologically closer to laterals) may suggest a dignathic heterodonty for this species. The species *Squalicorax intermedius* (Glikman in Glikman and Shvazhaite, 1971) (originally included in the genus *Palaeoanacorax*) was based on two poorly figured teeth from the Upper Turonian of Western Kazakhstan (Mangyshlak) but additional material from the type locality was subsequently attributed to this species (Glikman, 1980). One of the *S. intermedius* teeth (Glikman, 1980; pl. 12, fig. 6) is a latero-posterior tooth that exhibits comparable characters to those of *S. lalunaensis* sp. nov. but differs by its much more marked basal bulge of the labial crown face, wider main cusp, less differentiated mesial heel, less labio-lingually compressed aspect, and presence of serrations. Vullo et al. (2007) reported one tooth attributed to *Squalicorax* cf. *intermedius* that can be separated from those of the species described here by its strong serrations, wider and non-sigmoid main cusp and more rounded extremities of root lobes; along with its larger size. Glikman (1980, p. 99) erected the subspecies *Palaeoanacorax obliquus subserratus* based on the single latero-posterior tooth figured by Glikman (1964; p. 76, pl. 3, fig. 7) as *Palaeoanacorax falcatus* from the Cenomanian of Saratov (Russia). The cutting edges of this tooth appear smooth although the description reports irregular serrations on some specimens. In addition, the tooth figured by Glikman (1964) differs from those of *S. lalunaensis* sp. nov. by its shorter and wider main cusp, less marked convexity of the mesial cutting edge of main cusp and lower distal heel. *Squalicorax pamiricus* (Glikman *in* Glikman and Shvazhaite, 1971) was described on the basis of two crown fragments from the lower Turonian (Mammites nodosoides Zone) of Tajikistan but additional material from the type locality was figured by (Glikman, 1980), both under the genus name *Palaeoanacorax*. Teeth of this species bear serrations and can further be separated from *S. lalunaensis* sp. nov. by their more symmetrical root, wider and less sigmoid main cusp in lingual/labial views. Teeth of *S. pawpawensis* can be readily separated from those of *S. lalunaensis* sp. nov. by their less individualised mesial heel, presence of serrated cutting edges, more flared labial extremities of root lobes and less concave basal bulge of labial crown face with more numerous and finer indentations. Teeth of a number of nominal and unnamed small-sized *Squalicorax* species with smooth or irregularly serrated cutting edges may resemble those of *S. lalunaensis* sp. nov. Species of the *S. volgensis* group (including *S. volgensis* and an unnamed species from the Cenomanian–Turonian of Australia, Texas and upper Cenomanian of Kansas) are represented by teeth of comparable morphology with those of *S. lalunaensis* sp. nov. and these taxon are likely closely-related. However, teeth of this group of taxa differ from those of the species described here by their less mesio-distally expanded laterals, presence of weak and uneven serrations (see Siverson et al., 2007), smooth labial crown face in posteriors and mesial heel less individualised from the main cusp. *Squalicorax* aff. *pawpawensis* reported from the Cenomanian of Canada (Underwood and Cumbaa, 2010) is another small-sized anacoracid that is close to the *S. volgensis* group. This material have a less elongate main cusp and higher mesial heel.

Squalicorax aff. *lalunaensis* sp. nov.

Figures 5A-B

Material. One tooth (AMU-CURS-907) from Cementos Andinos quarry (Trujillo state).

Remarks. The single (lateral) tooth referred to this taxon resembles those of *S. lalunaensis* sp. nov. but differs by its larger size, more robust general aspect, much wider main cusp with convex distal edge, wider lingual neck, less marked notch separating the main cusp from the distal heel, wider labial angle between the main cusp and basal root face, higher root and presence of marked and irregular serrations on the mesial and distal cutting edges of main cusp and distal heel.

Squalicorax sp. 1

Figures 5C-I

Material. Three teeth (MBLUZ P-15, MBLUZ P-430-B, MBLUZ P-430-C) from La Luna quarry (Zulia state).

Description. The anterior tooth of this taxon is higher (8.5 mm) than wide (7.5 mm). The crown is composed of a fairly low and wide triangular main cusp that is slightly bent to the commissure and low and short distal heel. The main cusp is strongly convex lingually and flat labially with straight mesial and distal cutting edges. A thick lingual neck is present. The labial crown face bears a strongly marked labial bulge in its W-shaped basal edge that protrudes labially. The labial bulge is strongly scalloped by numerous notches where nutritive foramina of variable size open. Faint thin and short vertical folds are present on the labial bulge. The root is high and stocky with short and wide root lobes and slightly concave lateral edges in lingual view. Lateral and latero-posterior teeth are as high as wide, reaching 12.5 mm in maximum size. The main cusp is moderately inclined to the posterior with straight to slightly convex mesial cutting edge and straight distal cutting edge. The mesial heel is elongate and weakly demarcated from the main cusp by a slight concavity in lingual view. The distal heel is low and elongate. Both heels have their lateral extremities supported by a thin protuberance of the root oriented labially. The basal bulge of the labial crown face is strongly marked, labially oriented in the marginal regions and scalloped with short folds associated with larger but low enamelled protuberances. The root is fairly high with a large concavity of the basal edge separating two labially-oriented lobes. The mesial root lobe is shorter and thicker than the distal one, which exhibits a sharp mesial extremity. Several labial foramina are present both at the crown/root edge and below. All teeth bear large and regular serrations on the cutting edges and heels.

Remarks. Teeth of this taxon bear resemblances with those of *Squalicorax* sp. 3 described below but display differences including a less individualised mesial heel, wider and less labially convex main cusp, labial folds and more strongly and finely scalloped labial crown bulge and strongly labially oriented marginal regions of labial bulge. *Squalicorax* sp. 1 can be differentiated from *Squalicorax* sp. 4 by its teeth with higher root, more developed root lobes, straight mesial cutting edge of main cusp and more indented labial crown bulge. The taxon reported as *Squalicorax* sp. 1 from the upper Turonian of the Kwanza Basin in Angola by Antunes and Cappetta (2002) might be closely related to the species described here. However, the Angolan taxon differs in having less marked labial concavity of the root and narrow notch separating the main cusp from distal heel in lateral teeth and in the overall morphology of anteriors. This material cannot be assigned to any nominal *Squalicorax* species and likely represents a separated species.

Squalicorax sp. 2

Figures 5J-N

Material. Two teeth (AMU-CURS-892 and AMU-CURS-893) from Cementos Andinos quarry (Trujillo state).

Description. The two lateral teeth of this taxon are slightly wider than high, reaching maximum width of 12 mm. The triangular main cusp is large and bent to the commissure with a strongly convex lingual face and a slight convex labial face. The lower part of the labial face of main cusp bears a shallow vertical depression in its median region. The mesial cutting edge is slightly convex in lingual view whereas the distal cutting edge is straight. The mesial heel is elongate but low and undifferentiated from the cutting edge except by a light concavity. The distal heel is well developed and sub-horizontal with an uneven straight to slightly convex outline in lingual view. A very broad triangular-shaped lingual neck delimits the crown from the root. The basal region of the labial crown face bears a moderately developed bulge that tapers towards the marginal regions. The labial bulge is concave in its median part and indented by depressions where large labial foramina open. Cutting edges of the main cusp and heels bear thin, irregular and marked serrations that penetrate deep into the crown. The root is fairly low, mesio-distally developed and bilobate. The mesial root lobe is rather short with a sharp extremity whereas the distal lobe is more developed, thicker, with a blunt extremity. Both lobes are separated by a wide concavity of the basal root edge. The lingual crown face is low and exhibits a narrow and shallow central protuberance. A central foramina is present on the flat basal face, along with other foramina randomly located and of variable size.

Remarks. The overall tooth morphology of this taxon is relatively common among large mid-Cretaceous *Squalicorax* and the scarcity of the material recovered from La Luna Formation precludes finer taxonomic assignment. Most mid-Cretaceous *Squalicorax* teeth with comparable general morphology (e.g. relatively large teeth with strong serrations and fairly wide main cusp) were placed within - or put in close relationship within - either *Squalicorax curvatus* (Williston, 1900) or *Squalicorax falcatus* (Agassiz, 1843). This situation was in great parts due to the quality of the type series of both species, being represented by scarce incomplete specimens for the former and by drawings of a heterogenous series for the latter (see Siverson et al. 2007 for illustrations of the lectotype of *S. falcatus*). In addition, morphologies of these two taxa appear to be quite distinct when type materials are compared but teeth from some *Squalicorax* populations were frequently included, despite morphological differences, into one or both of these taxa (see Underwood and Cumbaa, 2010). Teeth of *Squalicorax* sp. 2 can be differentiated from those of *S. falcatus* by their narrower main cusp with straight distal cutting edge, less convex contact between the lingual crown face and root, more marked labial crown bulge and lower root with more developed lobes. Teeth of *S. curvatus* have a lower and much broader main cusp, higher heels with the mesial one being generally more individualised than in *Squalicorax* sp. 2. Specimens figured in Welton and Farish (1993, p. 116, figs. 1-2) as *S. curvatus* from the Cenomanian (Lewisville Member of the Woodbine Formation) of Texas fall outside of the range of variation of *S. curvatus* and are morphologically close to those of *Squalicorax* sp. 2. However, differences including less developed root lobes with shallower concavity of the basal root edge and higher lingual root face in the North American material separate both taxa. *Squalicorax obliquus* (Reuss, 1845) and *Squalicorax heterodon* (Reuss, 1845) are two species described from the Turonian of Czech Republic. In the original description of *S. heterodon*, Reuss (1845; p. 3, pl. 3, figs. 49-71) considered that all *Corax* (the former name of *Squalicorax*) species described by Agassiz (1843) excepted *Corax pristodontus* and *Corax appendiculatus* (with the exception of pl. 26 fig. 3) should be lumped into a single taxon. [It should be noted that parts of the material on which Agassiz based his species *C. appendiculatus* corresponds to the squaliform genus *Centrophoroides* (pl. 26a, figs. 18-20, *non* figs. 16-17, pl. 26, fig. 3 as *Galeus appendiculatus*), whereas the remaining specimens belong to the genus *Squalicorax*]. Consequently, he erected the species *S. heterodon* to accommodate this lumping, clearly stating that some of his material (pl. 3, figs 49-50, 52-53, 55-63, 65-68) corresponds to *S. falcatus*, others (pl. 3, figs. 51, 54) to *S. kaupi*, some specimens (pl. 3, figs. 64, 70) to *C. affinis* (now in the genus *Pseudocorax*), whereas he considered the remaining teeth (pl. 3, figs. 64, 70) to be close to *C. appendiculatus*. Although it is clear that the type series of *S. heterodon* is heterogeneous, the different species lumped into this taxon name do not correspond to those mentioned by Reuss and only a thorough re-examination of Reuss's material will allow the assessment of the identity of the species figured under the name *S. heterodon*. The species name *S. heterodon* cannot be considered valid and must be considered *nomen neglectum*. The species *S. obliquus* is based on three specimens (pl. 4, figs 1-3) from the Turonian of Czech Republic but Reuss himself indicated (Reuss, 1845; p. 4) that one specimen (pl. 4, fig. 2) might belong to a different species. Assessing the degree of morphological variation of this species is complicated as the material (pl. 4, figs 1, 3) is incomplete and might be morphologically close to some specimens figured in *S. heterodon*. Teeth of *Squalicorax* sp. 2 are morphologically close to the Reuss's specimen (pl. 4, fig. 2) but differ by their shorter distal heel. The crown of the incomplete most lateral tooth of *Squalicorax* sp. 2 but the root morphology of *S. obliquus* teeth is not known.

Squalicorax sp. 3

Figures 5O-S

? 1927 *Squalicorax baharijensis*; Stromer, pl. 1, fig. 26 *non* pl. 1, figs 25, 27.

? 1989 *Squalicorax baharijensis* Stromer; Werner, pl. 15, fig. 1 *non* pl. 14, figs 1-9 & pl. 15, figs 2-3.

Material. Two teeth (MBLUZ P-881 and MBLUZ P-430-D) from La Luna quarry (Zulia state).

Description. The anterior tooth is higher (10 mm) than wide (7.5 mm). The triangular main cusp is erect though slightly bent to the commissure with a nearly straight distal cutting edge and a slightly convex mesial cutting edge in its median region. The mesial heel is short, oblique, and poorly individualised from the main cusp. The distal heel is convex, fairly low and oblique, which contrasts with the vertical distal edge of main cusp. The lingual face of main cusp is strongly convex whereas the labial face is flat. A very wide lingual neck is present, reaching its maximum width in its median region. The lower area of the labial crown face is oriented labially and exhibits a marked labial bulge that overhangs the root in its central part. The basal edge of the labial crown face shows a fairly narrow and concave median area that bears five notches corresponding to the openings of labial root foramina. The labial marginal areas of the basal crown edge are convex. The cutting edges of main cups and heels bear relatively coarse serrations with the exception of the smooth lateral edges of the heels. The root is bilobate and V-shaped in basal view with a marked concavity of the basal edge of the labial crown face. The distal root lobe is wider with a more rounded distal edge in basal view. A central foramen is present onthe basal face, along with other smaller foramina over the basal surface. Large, oval-shaped labial foramina are present at (median area) or below (marginal areas) the root/crown edge. The lateral tooth is more mesio-distally elongate than the anterior and slightly higher (11 mm) than wide (10 mm). The mesial and distal cutting edges of the main cusp are fairly straight. A well-developed mesial heel is present, slightly oblique and fairly low. The distal heel is sub-horizontal, low and separated from the main cusp by a notch. The labial crown face is similar to that of the anterior tooth though more mesio-distally elongate with a less deep median concavity and more numerous notches where large labial foramina open. The root lobes are oriented laterally and form a shallow and wide concavity of basal root edge. The distal root lobe is shorter and wider than the mesial one. The basal root face is fairly flat. The mesial edge of the root is straight and oblique whereas the distal one bears a shallow notch below the crown/root edge. Below the labial crown bulge, the large oval-shaped foramina opening at the crown-root edge bear a thin veil of osteodentine over the enamelled edges. Other large and smaller foramina are present on the labial face.

Remarks. This taxon is represented by scarce material but exhibits tooth characters that differ from other *Squalicorax* species reported here. *Squalicorax* sp. 3 is morphologically close to *Squalicorax* sp. 1 described here from the same locality but differs by its more developed and individualised mesial heel (in laterals), narrower main cusp, labial crown face with less marked basal bulge and less labially oriented marginal areas, basal edge of labial crown face devoid of vertical folds. The size and morphology of the lateral tooth of *Squalicorax* sp. 3 is comparable to the specimen figured in the original description of *Squalicorax baharijensis* (Stromer, 1927) by Stromer (1927; pl. 1, fig. 26) and refigured by Werner (1989; pl. 15, fig. 1) from the upper Cenomanian of the Gebel Dist Member of the Bahariya Formation in Egypt, although the latter likely corresponds to a more lateral tooth file. As already noted by Siverson et al. (2007) the specimen illustrated by Werner (1989) strongly contrasts from the topotypic material of *S. baharijensis* she illustrated and probably represents a different species. Based on the scarce material from Egypt and Venezuela, it is preferable to leave this species in open nomenclature.

Squalicorax sp. 4

Figures 5T-V

Material. Two teeth (MBLUZ P-432 and MBLUZ P-432-B) from La Luna quarry (Zulia state).

Description. These lateral teeth is wider (11 mm) than high (8.5 mm) and exhibit a triangular main cusp bent to the posterior. The main cusp is biconvex but strongly labio-lingually compressed. The mesial edge of the main cusp is slightly convex and undifferentiated from the low mesial heel. The distal heel is low, convex and sub-horizontal with a marked demarcation from the main cusp. A rather large lingual neck is present. The basal edge of the labial crown face is concave in its median region where it bears a labial bulge, whereas the marginal edges are convex and less protruded. Rather coarse but irregular serrations are present on cutting edges and heels of the crown. Serrations reach maximum width in the lower part of the cutting edges and proximal part of the heels and taper near the apex of the main cusp. The root is low with fairly narrow lobes oriented laterally. The basal face is weakly concave in labial view and bears a central foramen and other foramina of variable sizes. The mesial and distal root edges are concave. The labial root face is pierced by several foramina, some of them being situated in very shallow notched of the labial crown bulge.

Remarks. This material shares features with teeth of *Squalicorax* sp. 2 from Cementos Andinos quarry. However, teeth of *Squalicorax* sp. 4 differ in having a more convex labial face of main cusp, marked labial angle between distal heel and main cusp, lower root (in labial view) with more symmetrical root lobes and thinner basal labial bulge of the crown. In addition to their smaller size, teeth of *Squalicorax* sp. 4 bear serrations that differ from those of *Squalicorax* sp. 2. In the latter (Fig. 5M), serrations penetrate deep into the crown in labial view and are thin, irregular and separated by rather wide depressed areas. Serrations of teeth of *Squalicorax* sp. 4 are rather large, blunt and separated by narrow notches (Fig. 5V). Teeth of *Squalicorax* sp. 4 differ from the laterals of *Squalicorax* sp. 3 from the same locality in being more labio-lingually compressed with no differentiated mesial heel, lower root, more convex labial face of main cusp, more symmetrical root lobes, more convex and oblique distal heel and less scalloped labial bulge. Teeth of *Squalicorax* sp. 4 have a more convex mesial cutting edge than laterals of *Squalicorax* sp. 1, lower root with thinner and less developed root lobes. The morphology of teeth of *Squalicorax* sp. 4 does not fall into the range of variation of any nominal or unnamed species published so far.

Family Cretoyrhinidae Glikman, 1958

Genus *Cretoxyrhina* Glikman, 1958

Cretoxyrhina mantelli (Agassiz, 1843)

Figures 6A-B

Material. One incomplete tooth (MBLUZ P-41) from La Luna quarry (Zulia).

Description. This tooth is cuspidate with a broad main cusp inclined distally. The labial cusp face is almost flat whereas the lingual face is markedly convex. A pair of oblique lateral heels is present, the distal one being less inclined and higher than the distal one. The heels bear no cusplets, although the mesial one is damaged, and the cutting edges are continuous from the main cusp to the lateral extremity of the heels. The crown lacks ornament but bears a faint central vertical fold at the base of the labial crown face. The labial crown very weakly overhangs the root in occlusal view. The base of the lingual crown face is marked by a rather thick neck that reaches its maximum thickness in its median part. The root is wide (25 mm), bilobate and asymmetrical with a more elongate, more oblique and thinner mesial lobe. The basal edge of the root is strongly concave. The lingual root face bears an acute lingual protuberance that is pierced by a central foramen. The lingual face of the distal extremity of the root lobes is nearly flat. Numerous oval-shaped labial foramina open below the basal edge of the crown and others are randomly situated over the labial face of the root lobes. Lingual foramina are present on the marginal faces, below the basal crown edge.

Remarks. The species *Cretoxyrhina mantelli* is known from a large number of Upper Cretaceous localities worldwide, but the specimen reported here represents the first record of the genus in South America. Numerous associated tooth sets have been described (Bourdon and Everhart, 2011; Shimada, 1997a; Welton and Farish, 1993) and the dentition and range of variation of this species is relatively well known. The specimen described here agrees with the morphology of *C. mantelli* and probably represents an upper lateral tooth. *Cretoxyrhina denticulata* (Glikman, 1957) is another species of this genus that occurs in the Cenomanian of Russia and North America (Underwood and Cumbaa, 2010), France (Vullo, 2015) and England (Guinot et al., 2013). This differs from *C. mantelli* in having lateral and posterior teeth of adult specimens with lateral cusplets and being smaller with a more stubby general aspect.

Family Odontaspididae Müller and Henle, 1839

Genus *Microcarcharias* gen. nov.

Derivation of name. After the small size of the teeth and their overall resemblance to the teeth of the modern lamniform shark *Carcharias* Rafinesque, 1810.

Type species. *Odontaspis saskatchewanensis* Case, Tokaryk and Baird, 1990 from the lower Turonian of Canada. The age of the type stratum was initially indicated as Coniacian in original publication but was subsequently revised to early Turonian (Cumbaa and Tokaryk, 1999; Underwood and Cumbaa, 2010).

Diagnosis. Odontaspidid possessing small (less than 6 mm high) and gracile teeth with gradient monognathic and dignathic heterodonty. Main cusp slender, biconvex, triangular and bent lingually. Pair of erect lateral cusplets in labial position relative to main cusp; wide and bulbous lower region of cusplets overhanging the root in marginal area; thin and needle-like in upper region, straight to slightly diverging. Cutting edges of main cusp thin and low, sometimes discontinuous with those of cusplets. Basal region of crown overhanging the root labially in occlusal view. Main cups with median vertical ridge occasionally present in lower region of labial face, connected to a slight bulge at the basal crown edge. Faint short vertical ridges on basal edge of labial crown face. Root holaulacorhize and bilobate with flared distal region of root branches. Strong lingual root protuberance with wide and deep nutritive groove pierced by large central foramen. Numerous large foramina on labial root face. Upper lateral teeth more inclined to the posterior, rarely with an additional mesial cusplet. Lower laterals with wider crown. Posterior teeth low with short and mesio-distally oriented root branches; basal root face flat. Lateral cusplets wide and short. Labial crown ornament of more or less pronounced vertical ridges on main cusp and cusplets.

Remarks. This genus adds to the diversity of small mid-Cretaceous lamniform sharks and can be separated from those by the following association of tooth characters: small size of teeth (the smallest of all known odontaspidids), marked lingual root protuberance, peculiar morphology of lateral cusplets, labial bulge of basal crown face and labial crown ornamentation. Teeth of the odontaspidid genus *Cenocarcharias* Cappetta and Case, 1999 are close in size and morphology to those of *Microcarcharias* gen. nov. but differ in their thicker main cusp with peculiar lingual wrinkles, wide lingual neck and wider and stouter lateral cusplets that not protrude labially relatively to the main cusp. Teeth of *Roulletia* Vullo, Cappetta and Néraudeau, 2007 can be differentiated from to those of *Microcarcharias* gen. nov. by their larger size, more robust general aspect, wide lower region of main cup, lack of labial crown overhang, poorly individualized cusplets and absence of crown ornamentation. *Johnlongia* Siverson, 1996 is another mid-Cretaceous odontaspidid genus whose teeth show a strong lingual protuberance and gracile and elongate main cusp. However, teeth of *Johnlongia* can be easily distinguished by their extremely developed lingual root protuberance with a rectangular shape in basal view, very high crown heels, rectilinear basal edge of the labial crown face and typical foraminifera on the margino-lingual root faces. Teeth of a few non-odontaspidids may resemble some of *Microcarcharias* gen. nov. Among them, the tentative archaeolamnid genus *Dallasiella* Cappetta and Case, 1999 has teeth that differ from *Microcarcharias* gen. nov. by their flatter labial crown face, lower and wider cusplets not protruding labially, less marked nutritive groove and thicker root lobes. *Haimirichia* Vullo, Guinot and Barbe, 2016 is another small mid-Cretaceous lamniform included in the family Haimirichiidae. Teeth of *Haimirichia* are easily separated from those of *Microcarcharias* gen. nov. less marked lingual root protuberance and nutritive groove, flat basal edge of the labial crown face, wide and developed root lobes in laterals with flat basal face with wider and shorted cusplets.

Microcarcharias saskatchewanensis (Case, Tokaryk and Baird, 1990) comb. nov.

Figures 6C-O

1974 *Odontaspis applegatei* Meyer, p. 201-202, fig. 64.

1990 *Odontaspis saskatchewanensis* Case, Tokaryk and Baird, p. 1085, figs 4-5.

1990 *Synodontaspis lilliae* Case, Tokaryk and Baird, p. 1085, fig. 6.

1993 *Carcharias* sp. A; Welton and Farish, p. 91, figs 1–6.

2001a *Carcharias saskatchewanensis* (Case, Tokaryk and Baird); Cicimurri, p. 36, fig. 7n;

2001b *Carcharias saskatchewanensis* (Case, Tokaryk and Baird); Cicimurri, p. 188, fig. 5q.

2006 *Carcharias saskatchewanensis* (Case, Tokaryk and Baird); Shimada et al., p. 11, figs 9.3-9.4.

2006 *Carcharias tenuiplicatus* (Cappetta and Case, 1975); Shimada et al., p. 13, figs 9.5-9.6.

2008 *Carcharias saskatchewanensis* (Case, Tokaryk and Baird); Shimada and Martin, p. 92, fig. 5H.

Material. Two teeth (AMU-CURS-890 and AMU-CURS-891) from Cementos Andinos quarry (Trujillo state) and three teeth (MBLUZ P-14, MBLUZ P-433 and MBLUZ P-14-B) from La Luna quarry (Zulia state).

Description. Teeth of this species are small, not exceeding 6 mm high. Teeth from the anterior files are sub-symmetrical with a narrow triangular main cup that is erect and bent lingually. The main cusp is biconvex and bears very thin and low cutting edges that become very thin or fade out on the heels. The heels are strongly inclined basally and bear a pair of lateral cusplets. Lateral cusplets are erect or slightly diverging, oriented lingually and conical with a wide lower region that thins out in the upper half. Cusplets are well separated from the main cusp and in labial position relatively to the main cusp. The basal edge of the labial crown face bears a bulge that is more marked below the heels than in its central part. A thin lingual neck separates the lingual crown face from the root. The root is holaulacorhize and bilobate with well-developed root branched that are inclined basally. Root branches become thinner distally and largely overtake the labial edge of the heels. The lingual root protuberance is marked and separated by a wide nutritive groove that is pierced by a large central foramen. The marginal regions of the lingual root face bear numerous foramina that are aligned just below the crow/root edge. The labial root face is high, abrupt, and pierced by several wide foramina including a large central foramen. Teeth from antero-lateral files are more asymmetrical in upper files than in lower files. Teeth from these files can show a narrower and more protruding lingual protuberance of the root. The distal extremity of the root lobes is slightly bent basally. The mesial root lobe is shorter and wider than the distal one. The labial face of the main cusp can show a thin median vertical ridge in lower region ending in a slight bulge at the basal edge of the crown. Some faint labial vertical ridges are irregularly distributed below the distal edge of the cusplets and poorly marked folds can be present on the basal edge of the labial crown face, on both sides of the labial buldge.

Remarks. In addition to the description of the species *Microcarcharias saskatchewanensis* comb. nov., Case et al. (1990) described the species *Synodontaspis lilliae* Case, Tokaryk and Baird, 1990 on the basis of two teeth from the same locality. The authors only figured the holotype represented by a lateral tooth. Comparing this specimen with laterals of *M. saskatchewanensis* comb. nov. subsequently reported from the Cenomanian of Texas (Welton and Farish, 1993) and Colorado (Shimada et al., 2006 as *Cenocarcharias tenuiplicatus*) indicate that the holotype of *S. lilliae* is a lateral tooth of *M. saskatchewanensis* comb. nov. Consequently, we consider the species *S. lilliae* a junior synonym of *M. saskatchewanensis* comb. nov. This species has been reported from a number of Cenomanian to lower Turonian localities in the Western Interior Seaway: lower Turonian of Canada (Case et al., 1990), Cenomanian (Eagle Ford Group, Britton Formation) of Texas (Welton and Farrish, 1993: p. 91; Meyer 1974), Colorado (Shimada et al., 2006), Kansas (Shimada and Martin 2008) and S. Dakota (Cicimurri, 2001a, 2001b). The material reported here represents the southernmost record of this species and the first outside the WIS.

Family Otodontidae Glikman, 1964

Genus *Cretolamna* Glikman, 1958

Cretolamna sp.

Fig. 6P

Material. One incomplete tooth (MBLUZ P-86) from La Luna quarry (Zulia state).

Description. The single specimen recovered is an incomplete tooth embedded in matrix with only the labial face being observable. The tooth is wider (14 mm) than high, although the apex of the crown is lacking. The main cusp is triangular and inclined to the posterior with a convex labial face except in its central region where a vertical concavity is present at the base of the cusp. A pair of low and broad lateral cusplets is present, separated from the cutting edges of the main cusp by a narrow notch. The mesial cusplet is diverging and bears an incipient secondary cusplets in its mesial edge. The distal cusplet is incomplete but both mesial and distal marginal cusplets bear a blade-like extension of enameloid that exceeds the lateral edges of the root. The basal edge of the labial crown face is flat except in the median region where a slight bulge is present. The labial crown face is devoid of ornamentation apart from very faint and short vertical folds at the basal edge of the crown. The labial root face is flat to slightly concave in profile view shows two large and triangular-shaped lobes separated by a narrow v-shaped notch. Both lobes bear a protuberance on the angle between their lateral and basal root edges. Numerous large and oval-shaped foramina open on the labial root face.

Remarks. The genus *Cretolamna* is amongst the most commonly reported lamniforms in post-Aptian Cretaceous deposits. Most Cretaceous records of this genus (and several younger records) were assigned to the species *Cretolamna appendiculata* (Agassiz, 1843). Yet, this species was based on a heterogeneous series that lumped several different species and genera with unclear stratigraphic and precise geographic details, which led Siverson (1999) to designate a lectotype. A much needed revision of Late Cretaceous *Cretolamna* (Siversson et al., 2015) untangled a large part of the taxonomic lumping within this genus and concluded that the species *C. appendiculata sensu stricto* should be restricted to the material from the type area (Cenomanian-Coniacian of Lewes, England) and lower Turonian of France (Bettrechies). Because of the difficulties in identifying *Cretolamna* material at species level even based on numerous well-preserved specimens, we prefer to leave the specimen described here in open nomenclature.

Although Upper Cretaceous records of *Cretolamna* are frequent worldwide (see Cappetta, 2012), reports of this genus from South America are scarce. Previous reports include an abraded tooth from the Maastrichtian of Argentina attributed to *C. appendiculata* (Bogan and Agnolin, 2010) and *Cretolamna biauriculata* (Wanner, 1902), from the Maastrichtian of Brazil (Rebouças and Silva Santos, 1956). The tooth described here indicates the presence of the genus *Cretolamna* from South America as soon as in the earliest Late Cretaceous.

Lamniformes *incet. sedis*

Genus *Acutalamna* gen. nov.

Derivation of name. From the latin *acutus* (sharp, pointed) in allusion to the elongated and sharp morphology of the crown.

Type species. Acutalamna karsteni gen. et sp. nov.

Diagnosis. Lamniform with gradient monognathic heterodonty. Cuspidate teeth higher than wide. Slender main cusp weakly (anterior teeth) to strongly (laterals) bent distally, devoid of lateral cusplets; main cup sigmoid in labial and profile views. Lateral heels oblique in anterior teeth; mesial heel incipient to absent in more lateral tooth files. Cutting edges smooth, low and thin. Large crown neck. U-shaped root of anaulacorhize stage. Root bilobate, asymmetrical with more developed and thinner mesial lobe; strong and protruding lingual protuberance with central foramen. Labial root face with variable number of foramina below the crown/root edge. More lateral teeth strongly asymmetrical with short and stubby mesial root lobe and incipient or no mesial crown heel; basal root edge curved and wide. Heels absent in latero-posterior teeth.

Remarks. The genus *Priscusurus* Kriwet, 2006 was erected on the type species *Priscusurus adruptodontus* Kriwet, 2006 from the ?middle Albian (Muerto Limestone Fm.) of northwestern Peru. Yet, the type series mainly includes incomplete teeth and appears to be heterogeneous. The holotype (BMNH P. 36287) of *P. adruptodontus* is a complete tooth embedded in matrix of which only the lingual face is observable. This tooth shows characters of anacoracid lamniforms (flat basal face of the root, poorly differentiated root lobes, labio-lingually compressed root, concave marginal areas of the lingual root face and triangular-shaped crown) that are typically found in *Squalicorax* species. Other teeth (?Fig 2B-C and Fig. 3J) also belong to the genus *Squalicorax*. Consequently, as the holotype is the bearer of the scientific name a species-group taxon (ICZN Art. 72.10), the species *adruptodontus* must be transferred to the genus *Squalicorax*. However, since the holotype of *S. adruptodontus* comb. nov. (Kriwet, 2006) is embedded in matrix and represents a species of *Squalicorax*, an extremely diverse genus comprising 53 nominal species (Cappetta et al., 2014) with high variability in tooth morphologies, the figured specimens are not sufficient to justify the validity of the species. Accordingly, *S. adruptodontus* comb. nov. (Kriwet, 2006) should be considered *nomen dubium.* In the absence of type species for the genus *Priscusurus*, this genus name should be considered *nomen nudum* and the non-*Squalicorax* teeth of the original type series of *Priscusurus adruptodontus* should be included in an unnamed species of the genus *Acutalamna* gen. nov. (see below).

Additional species. Excluding the specimens originally assigned to *Priscusurus adruptodontus* from the Albian of Peru (Kriwet, 2006) that correspond to the *nomen dubium* species *S. adruptodontus* comb. nov. results in a series (Fig. 2B-C *non* Fig. 2A & ?Fig 2B-C, Fig. 3A-I *non* Fig. 3J) composed of fragmentary specimens that make difficult the identification of the material at the species level. Consequently, although the morphology of these teeth corresponds to an *Acutalamna* species, it is preferred to leave it in open nomenclature. Cappetta (2012) figured two teeth attributed to *Priscusurus adruptodontus* from the upper Albian of Ecuador. The material was originally said to come from Peru but was actually collected from the Napo Fm. (Western Oriente Basin) of Ecuador (Cappetta pers. com. 2017) and reported as "undetermined lamniform probably representing a new genus" (Jaillard, 1997; p. 58). While the material from Peru (Kriwet, 2006) here attributed to *Acutalamna* sp. corresponds to lateral to latero-posterior teeth, specimens from Ecuador are represented by anterior and antero-lateral teeth. Hence, it is possible that they correspond to the same taxon but the lack of comparable specimens between the two localities and the fragmentary state of preservation of the Peruvian material precludes certain judgement. Biddle (1993) figured two teeth (pl. 4, figs. 19-20) as ?*Microcorax* sp. from the middle Albian of France. These show a bulky and asymmetrical root with a strong lingual protuberance and wide lingual neck as well as a sigmoid main cusp with wide lower part. These characters allow the attribution of these specimens to the genus *Acutalamna* gen. nov. However, teeth from France differ from the other Albian specimens by their more robust general morphology and probably correspond to a different, unnamed species. Cappetta (2012) proposed that the material figured by Dalinkevičius (1935, p. pl. 5, figs. 114-118) as *Oxyrhina* (?) *primaeva* from the Albian of Lithuania might be included in the genus *Priscusurus* (now *Acutalamna* gen. nov.). Yet, one of these specimens (pl. 5, fig. 118) was designated by Landemaine (1991) as the holotype of the species *Squalicorax primigenius* Landemaine, 1991 whereas the remaining specimens (pl. 5, figs. 114-117) present characters typical of the genus *Acrolamna* Zhelezko, 1990 (labio-lingually compressed teeth with no lingual root protuberance, wide and short root lobes, wide triangular main cusp) and should be included within this genus. The genus *Acutalamna* gen. nov. described here includes a single nominal species (*Acutalamna karsteni* gen. et sp. nov.) and ranges from the Albian to the Cenomanian.

Acutalamna karsteni gen. et sp. nov.

Fig. 7

Derivation of name. In honour of Hermann Karsten a 19th century German naturalist who conducted a pioneer exploration in northern South America and collected a number of palaeontological material from the Cretaceous and Pleistocene of Colombia and Venezuela (Carrillo-Briceño et al., 2016).

Holotype. AMU-CURS-908.

Type stratum. Laminated black/dark-grey shales in the basal part of the La Aguada Member, La Luna Formation.

Material. Six teeth (AMU-CURS-908 to AMU-CURS-913) from Cementos Andinos Quarry (Trujillo state) and one tooth (MBLUZ P-431) from La Luna Quarry (Zulia state).

Diagnosis. As for genus.

Description. Anterior teeth are cuspidate, higher (10 mm) than wide (5 mm), slender and gracile. The crown is composed of an elongate and lingually-inclined main cusp that is slightly bent distally and a pair of lateral heels. The lingual face of the cusp is strongly convex whereas the labial face is slightly convex to nearly flat with an incipient basal bulge. The crown heels are inclined basally with the mesial heel being more oblique than the distal one. Cutting edges are thin but sharp and run continuously from the apex of the main cusp to the lateral margins of the heels. The upper part of the crown is bent labially and shows a slight twisting, which confers a sigmoid shape to the main cusp in profile view. The crown/root edge of the lingual face bears by a thick neck. The root is anaulacorhize, bilobate and U-shaped in lingual/labial view with a concave basal face in profile view. Root branches are individualized and oriented labially. The mesial root lobe is slenderer and more elongate that the distal one. The lingual root face bears a strong and wide lingual bulge that is pierced by a wide central foramen. Numerous small foramina open on the lingual root face, immediately below the neck. The labial root face bears a few foramina in central position and others more irregularly open on the lingual face of the root lobes. Teeth from more lateral files have a more robust general morphology. The main cusp is wider in its lower part and has a more marked sigmoid outline in both lingual and profile views. The labial crown face is convex with a basal bulge. The distal heel is incipient or absent whereas the mesial heel is low and less oblique than in anterior teeth. The root is compact with strongly asymmetrical lobes that are well separated by an arched basal edge. The lingual root bulge is wide and strongly protrudes lingually but is less differentiated from the root lobes than in anterior teeth. The mesial root lobe is elongate whereas the distal one is short and stubby, sometimes poorly differentiated from the rest of the root. A series of foramina underline the labial crown bulge, sometimes associated with more irregularly situated foramina near the basal root edge. Latero-posterior teeth are low with incipient distal root lobe and no differentiated crown heels.

Remarks. Teeth of *Acutalamna karsteni* gen. et sp. nov. differ from the unnamed species from Ecuador (Cappetta, 2012) by their more marked and more individualized lingual protuberance. The specimens reported from the Albian of France (Biddle, 1993) differ from *Acutalamna karsteni* gen. et sp. nov. by their more robust general aspect, more mesio-distally compressed root and less elongate main cusp with a wider basal region. The single (antero-lateral) tooth recovered from La Luna Quarry is a museum specimen that could not be extracted from the sediment, nonetheless the observable features present on the lingual face allows attribution of this specimen to *A. karsteni* gen. et sp. nov. The material described here represents the last occurrence of the genus which is otherwise known only from the upper Albian of Ecuador (Cappetta, 2012) and ?middle Albian of Peru (Kriwet, 2006) and middle Albian of France (Biddle, 1993).

5. Discussion

5.1. Stratigraphy and palaeobiogeography

The specimens described here were sampled from two horizons within the La Luna Formation: one from the Aguada Member (Cementos Andinos Quarry, Trujillo state) and the other from just above the contact between the Maraca Formation (Cogollo Group) and the La Luna Formation (La Luna Quarry, Zulia state). While a Cenomanian age was proposed for the Aguada Member based on foraminifera and ammonites (Renz, 1959), the presence of horizons of Cenomanian age in the Maracaibo Basin, from which the La Luna Quarry samples originate, has been controversial (Dot et al., 2015; Erlich et al., 1999; Renz, 1982). The two sampled localities have distinct (and rich) anacoracid composition but they share two taxa: *M. saskatchewanensis* and *A. karsteni*. Despite its small-sized teeth, *M. saskatchewanensis* was collected from various Cenomanian fossil-rich horizons in the Western Interior Seaway (WIS) as well as from one lower Turonian locality in the WIS (see above). *Acutalamna* remains were so far known exclusively from the middle-upper Albian by at least two unnamed species groups (one from South America represented by two closely-related, if not conspecific, morphs and one from France). In addition, the La Luna quarry also yielded the species *Squalicorax* sp. 3, to which some material from the upper Cenomanian of Egypt has been referred (see above). Although the Cementos Andinos quarry and the La Luna quarry faunas are probably not contemporaneous, the presence of *M. saskatchewanensis* and *A. karsteni* in both localities and of *Squalicorax* sp. 3 in the Maracaibo Basin suggest a Cenomanian age for the base of the La Luna

Formation in this region. This is consistent with the suspected presence of upper Cenomanian strata forming the base of the La Luna Formation in the northwestern and central parts of the Maracaibo Basin, where rocks of La Luna Formation unconformably rest on upper Albian rocks (Erlich et al., 2000, 1999).

Microcarcharias saskatchewanensis was a small, probably nectobenthic shark typical of the Western Interior Seaway fauna and its presence in Venezuela suggests marine connexions between the WIS and the La Luna Sea. In addition, *Squalicorax moodyi* sp. nov. (La Luna quarry) is morphologically close to *Squalicorax* sp. from the upper Albian of Texas Welton and Farish (1993; p. 120) and *S. lalunaensis* sp. nov. (Cementos Andinos quarry) is close to the *S. volgensis* group (upper Cenomanian of Australia and Kansas) and to *Squalicorax* aff. *pawpawensis* from the Cenomanian of Canada (Underwood and Cumbaa, 2010). Although *C. mantelli* and *Cretolamna* species are very common in the Cenomanian of North America, these are cosmopolitan taxa that might not be reliable for palaeobiogeographic interpretations. However, the ichthyodectiform fish *Xiphactinus* Leidy, 1870 reported from Cementos Andinos quarry (Carrillo-Briceño et al., 2012) is another taxon typically found in the WIS. These occurrences suggests more affinities in fauna composition with the North American WIS than with African assemblages (see Antunes and Cappetta, 2002) although the *Squalicorax* sp. 3 specimen from La Luna Formation is morphologically close to the Cenomanian taxon reported from Egypt (Stromer, 1927; pl. 1, fig. 26). The lamniform assemblage reported here shows little similarities with taxa reported from other Southern Continents. An early Cenomanian selachian assemblage from South India (Underwood et al., 2011) yielded a single *Squalicorax* species (*Squalicorax* aff. *baharijensis*) that does not compare with the La Luna *Squalicorax* species along with teeth belonging to the cosmopolitan *Cretolamna appendiculata* group. Most other lamniform and non-lamniform sharks present in the Indian assemblage have anti-tropical distributions, which suggests that temperature, along with endemism, might explain differences in lamniform composition between these assemblages. Higher latitudes may also explain the differences in lamniform composition of selachian assemblages from Australia (Siverson, 1999, 1997, 1996) that comprise a high taxic diversity but very few anacoracids including representatives of the *S. volgensis* group. According to Erlich et al. (2000) the La Luna Sea was situated in a restricted basin surrounded by topographic highs that restricted connexions excepted in the north/northeast part. The lamniform material described here indicates some degree of endemism (anacoracids) that agrees with the restricted conditions of the sea and also indicates some connexions with northern seas. These marine connexions with northern oceans were certainly continuous through most of the Late Cretaceous as some other taxa reported from younger parts of the La Luna Formation such as the probably Coniacian *Ptychodus atcoensis* (Carrillo-Briceño and Lucas, 2013) and the Cenomanian-Santonian *Ptychodus cyclodontis* (Carrillo-Briceño, 2009) are known from the Coniacian of North America (Hamm, 2009) and the Turonian of the Caribbean (Mutter et al., 2005), respectively.

5.2. Palaeoenvironment and palaeoecology

La Luna Formation has been interpreted as a typical marine environment where laminated organic-rich intervals suggest a deposition in the mid-shelf to upper continental slope under anoxic or poorly oxygenated conditions (e.g. Bralower and Lorente, 2003; Erlich et al., 1999; Macellari and De Vries, 1987; Zapata et al., 2003). According to Tribovillard et al. (1991), the rich organic matter of the sediments in the La Aguada Member (Andes of Trujillo and Lara states) is of algal origin. González de Juana et al. (1980) suggested that the La Aguada Member could be considered as a transitional environment between the shallow waters of the Maraca formation (or La Puya Member according to Renz, 1968, 1959) and the pelagic facies of the La Luna Formation. Erlich et al. (1999) and Méndez (1981) suggested that the anoxic conditions of the La Luna Formation during the late Albian-early Cenomanian transgression were not due to water depth but to pre-existing anoxic conditions in the slope zone. On basis of benthic and planktonic foraminifera, Méndez (1981) recognized an increase in the submersion of the platform, but probably with depths that did not exceed 50 m.

Strata of the Aguada Member in Cementos Andinos quarry, especially the laminated black/dark-grey shales, yielded abundant bony fish remains represented by scales and isolated and semi-articulated cranial and postcranial elements of *Xiphactinus* (Carrillo-Briceño et al., 2012), other ichthyodectiforms, enchodontids and small indeterminate fishes. Marine sauropsids are represented in the locality by a single taxon, *Lunaophis aquaticus* Albino, Carrillo-Briceño and Neenan, 2016, a marine snake that exploited tropical environments. According to our own observations, benthic invertebrates are scarce in the shales of the Cementos Andinos quarry with only small bivalve moulds in the limestones (along with undetermined ammonites) and some inoceramids in the calcareous concretions. This could suggest periods of better oxygenated conditions on the sea floor for the La Aguada Member or may indicate that these organisms were tolerant to anoxic environments, as suggested for other sections of the La Luna Formation (e.g., Tribovillard et al., 1991). Although it is somewhat difficult to suggest a specific palaeoenvironment for this section of the La Aguada Member using the known vertebrate assemblage, the abundant fish remains may suggest well-oxygenated surface waters being part of a stratified water column. In La Luna Quarry, Moody and Maisey (1994) reported abundant fish remains (e.g. enchodontids, *Belonostomus*, *Bananogmius* and unidentified teleost scales and bones), and our sample from dissolved rocks yielded abundant disarticulated osteichthyan microremains. Although there is no clear environmental definition for this section using fossil assemblages, the Cenomanian rocks of the La Luna Formation in the Sierra de Perijá were considered representative of outer shelf to upper slope deposits (Erlich et al., 1999).

The most striking feature of the lamniform assemblages reported here is the high diversity of this group in the Cenomanian La Luna Sea with 12 species representing five families. In addition, a semi-complete (1.2 metres long), articulated vertebral column of a possible lamniform shark was also found *in situ* in the Cementos Andinos quarry. However, this specimen has been destroyed by quarry workers before being studied and only photographs were available to us. Nevertheless, one specimen figured here (CURS-893) and referred to *Squalicorax* sp. 2 was collected from the same layer, less than 20 cm from the vertebrae, which possibly indicates that the articulated vertebral column might belonged to a *Squalicorax*. While the palaeoecology of *Acutalamna* is not well known (although its tooth morphology suggests a nectobenthic predator or scavenger), the remaining taxa recovered represent various habits. The tooth morphology and anatomy of *Cretoxyrhina mantelli* suggest that this shark was an active pelagic predator feeding on large vertebrate preys (Shimada, 1997b), whereas there are numerous evidences of scavenging of large marine vertebrates (plesiosaurs, mosasaurs, turtles, large actinopterygians) by different *Squalicorax* species in the Late Cretaceous (Dortangs et al., 2002; Everhart, 2005; Schwimmer et al., 1997; Strganac et al., 2015). Feeding habits of *Cretolamna* species are more difficult to assess as the species diversity of this genus with a long stratigraphic range is probably underestimated. However, a report of numerous teeth of "*C. appendiculata*" around an elasmosaurid carcass from the Santonian of Japan (Shimada et al., 2010) suggests that at least some of the *Cretolamna* species happened to prey on dead carcasses, either occasionally or exclusively. *Microcarcharias saskatchewanensis* exhibits very small teeth of tearing type, which indicate a small nectobenthic predator probably feeding on small bony fishes and invertebrates. The dominance of anacoracids in La Luna quarry (four *Squalicorax* species) and Cementos Andinos quarry (three *Squalicorax* and one probable *Nanocorax* species) is correlated with the apparent high diversity of medium to large marine vertebrates found in association, which is consistent with their probable opportunistic feeding strategy (active predation and scavenging). Comparably high anacoracid diversity is known in mid-Cretaceous chondrichthyan assemblages from the WIS (Bice and Shimada, 2016; Cappetta and Case, 1999; Siverson et al., 2007; Welton and Farish, 1993), which also generally co-occur with large marine vertebrates. However, WIS assemblages mostly represent shallow to inner shelf epicontinental marine environments that contrast with the palaeoenvironments suggested for the La Luna Sea in the Cenomanian. The anacoracid material reported here indicates that the outer shelf/upper slope environments of the La Luna Sea were favorable to these sharks during the earliest Late Cretaceous. Previous reports of anacoracids from deep marine environments were restricted to the uppermost Cretaceous of Angola (Antunes and Cappetta, 2002) and Israel (Lewy and Cappetta, 1989). The assemblages described here indicate that anacoracids were adapted to outer shelf/slope marine environments early in their evolutionary history. The contrast in palaeoenvironments between the La Luna Sea and the WIS (although some species present in both regions are closely related, see above) might partly explain the differences in anacoracid composition of respective assemblages. However, this may also be due to differences in stratigraphic origins of theses assemblages, suggesting that anacoracid evolutionary rates were high in the mid-Cretaceous. This is a likely possibility given the large number of unnamed species from the North American mid-Cretaceous.

6. Conclusions

This contribution is the first report of chondrichthyans from the mid-Cretaceous of Venezuela and one of the few records of this group from the Cenomanian of South America. Two sampled sites within the La Luna Formation yielded twelve lamniform species including a number of new taxa. Comparisons between these assemblages and others suggests a Cenomanian age for the base of the La Luna Formation in the Maracaibo Basin. The composition of these assemblages indicates some degree of endemism in the La Luna Sea that agrees with the restricted environmental conditions proposed for this sea, but also suggests more probable connexions with the Western Interior Seaway than with Southern Continent seas. The anacoracid diversity of these assemblages is strikingly high (eight species in total) despite the outer shelf/upper slope palaeoenvironments of the La Luna Formation. The high diversity of these opportunistic predators is probably related to the high diversity of large marine vertebrates reported from these localities, which provided abundant food resources.

Acknowledgments

We are grateful to the geologists Carlos Torres, Engelberth Montilla, Crisanto Silva, Norelis Valera, and Cementos Andinos CA., for generous and significant collaboration during fieldwork. Tito Barros, Gilson Rivas and John Moody, are thanked for support and permission to study the specimens housed in the Museo de Biología de La Universidad del Zulia. Anne-Lise Charruault (ISE-M, University of Montpellier) helped with the restauration of some specimens from Trujillo state. To the Instituo del Patrimonio Cultural de Venezuela gave permissions for collecting and studying the specimens. Marcelo Sánchez-Villagra provided generous economical support and collaboration during fieldwork activities. The reviewers (C.J. Underwood and R. Vullo) and Editor are thanked for their comments on an earlier version on the manuscript.

References

Agassiz, L., (1833-44). Recherches sur les poissons fossiles 3, 422.

Albino, A., Carrillo-Briceño, J.D., Neenan, J.M., 2016. An enigmatic aquatic snake from the Cenomanian of Northern South America. PeerJ 4, e2027. doi:10.7717/peerj.2027

Antunes, M.T., Cappetta, H., 2002. Sélaciens du Crétacé (Albien-Maastrichtien) d'Angola. Palaeontographica Abteilung A 264, 85–146.

Berg, L.S., 1958. System der rezenten und fossilen Fischartigen und Fische. Deutscher Verlag Wissenschaft, Berlin, 310 pp.

Bice, K.N., Shimada, K., 2016. Fossil marine vertebrates from the Codell Sandstone Member (middle Turonian) of the Upper Cretaceous Carlile Shale in Jewell County, Kansas, USA. Cretaceous Research 65, 172–198. doi:10.1016/j.cretres.2016.04.017

Biddle, J.-P., 1993. Les élasmobranches de l'Albien inférieur et moyen (Crétacé inférieur) de la Marne et de la Haute-Marne (France), in: Herman, J., Van Waes, H. (Eds.), Professional Paper of the Belgian Geological Survey. Professional Paper of the Belgian Geological Survey, Brussels, pp. 191–240.

Bogan, S., Agnolin, F.L., 2010. Primera ictiofauna marina del Cretácico Superior (Formación Jaguel, Maastrichtiano) de la provincia de Río Negro, Argentina. Papéis Avulsos de Zoologia (São Paulo).

Bonaparte, C.L.J.L., 1838. Selachorum tabula analytica. Nuovi Annali delle Scienze Naturali 1, 195–214.

Bourdon, J., Everhart, M.J., 2011. Analysis of an associated *Cretoxyrhina mantelli* dentition from the Late Cretaceous (Smoky Hill Chalk, Late Coniacian) of western Kansas. Transactions of the Kansas Academy of Science 114, 15–32.

Bralower, T.J., Lorente, M.A., 2003. Paleogeography and Stratigraphy of the La Luna Formation and Related Cretaceous Anoxic Depositional Systems. PALAIOS 18, 301–304. doi:10.1669/0883-1351(2003)018<0301:PASOTL>2.0.CO;2

Brito, P.M., Janvier, P., 2002. A ptychodonid (Chondrichthyes, Elasmobranchii) from the Upper Cretaceous of South America. Geodiversitas 24, 785–790.

Brito, P.M., Leal, M.E.C., Gallo, V., 2013. A new Lower Cretaceous guitarfish (Chondrichthyes, Batoidea) from the Santana Formation, northeastern Brazil. Boletim do Museu Nacional. Nova serie geologia 1–14.

Brito, P.M.M., Ferreira, P.L.N., 1989. The first Hybodont shark, *Tribodus limae* n. gen., n. sp., from the Lower Cretaceous of Chapada do Araripe (North-East Brazil). Anais da Academia Brasileira de Ciências 61, 53–57.

Cappetta, H., 2012. Chondrichthyes - Mesozoic and Cenozoic Elasmobranchii: Teeth, Handbook of Paleoichthyology. Verlag F. Pfeil, Munich.

Cappetta, H., 2006. Elasmobranchii Post-Triadici (index specierum), Fossilium Catalogus I: Animalia. Blackhuys Publishers, Leiden.

Cappetta, H., Adnet, S., Akkrim, D., Amalik, M., 2014. New *Squalicorax* species (Neoselachii: Lamniformes) from the Lower Maastrichtian of Ganntour phosphate deposit, Morocco. Palaeovertebrata 38, e3.

Cappetta, H., Case, G.R., 1999. Additions aux faunes de sélaciens du Crétacé du Texas (Albien supérieur-Campanien). Palaeo Ichthyologica 9, 5–111.

Cappetta, H., Case, G.R., 1975. Sélaciens nouveaux du Crétacé du Texas. Geobios 8, 303–307.

Carrillo-Briceño, J.D., 2009. Presencia del género "*Ptychodus*" (Elasmobrachii: Ptychodontidae) en el cretácico superior de los Andes de Trujillo, Venezuela. Geominas 37, 207–210.

Carrillo-Briceño, J.D., Alvarado-Ortega, J., Torres, C., 2012. Primer registro de *Xiphactinus* Leidy, 1870 (Teleostei, Ichtyodectiformes) en el Cretacico superior de América del Sur (Formacion La Luna, Venezuela). Revista Brasileira de Paleontologia 15, 327–335.

Carrillo-Briceño, J.D., Amson, E., Zurita, A., Sánchez-Villagra, M.R., 2016. Hermann Karsten (1817–1908): a German naturalist in the Neotropics and the significance of his paleovertebrate collection. Fossil Record 20, 21–36. doi:10.5194/fr-20-21-2016

Carrillo-Briceño, J.D., Ayala, R., Chavez, E.O., Gonzalez, G., 2008. Registro de *Serratolamna serrata* (Elasmobranchii: Serratolamnidae) en el Cretácico Superior (Maestrichtiense) de los Andes Venezolanos. Geominas 36, 160–163.

Carrillo-Briceño, J.D., Lucas, S.G., 2013. The first tooth set of *Ptychodus atcoensis* (Elasmobranchii: Ptychodontidae), from the Cretaceous of Venezuela. Swiss J Palaeontol 132, 69–75. doi:10.1007/s13358-013-0053-3

Case, G.R., Tokaryk, T.T., Baird, D., 1990. Selachians from the Niobrara Formation of the Upper Cretaceous (Coniacian) of Carrot River, Saskatchewan, Canada. Can. J. Earth Sci. 27, 1084–1094. doi:10.1139/e90-112

Casier, E., 1947. Constitution et évolution de la racine dentaire des Euselachii. II-Etude comparative des types. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 23, 1–32.

Cicimurri, D.J., 2001a. Cretaceous elasmobranchs of the Greenhorn Formation (middle Cenomanian-middle Turonian), western South Dakota, in: Santucci, V.L., McClelland, L. (Eds.), Proceedings of the 6th Fossil Ressource Conference. Geologic Resources Division Technical Report.

Cicimurri, D.J., 2001b. Fossil selachians from the Bell Fourche Shale (Cretaceous, Cenomanian), Black Hills region of South Dakota and Wyoming. Mountain Geologist 38, 181–192.

Compagno, L.J.V., 1990. Relationships of the megamouth shark, *Megachasma pelagios* (Lamniformes: Megachasmidae), with comments on its feeding habits. National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service 90, 357–379.

Compagno, L.J.V., 1977. Phyletic relationships of living sharks and rays. American Zoologist 17, 303–322.

Cumbaa, S.L., Tokaryk, T.T., 1999. Recent discoveries of Cretaceous marine vertebrates on the eastern margins of the Western Interior Seaway, p. 57–63. In Summary of Investigations 1999. Volume 1. Miscellaneous Report 99-4.1. Saskatchewan Geological Survey, Saskatchewan Energy Mines.

Dalinkevičius, J.A., 1935. On the fossil fishes of the Lituanian chalk. I. Selachii. Mémoires de la Faculté des Sciences de l’ Universite de Vytautas le Grand 9, 247–305.

Davis, C., Pratt, L.M., Sliter, W.V., Mompart, L., Murat, B., 1999. Factors influencing organic carbon and trace metal accumulation in the Upper Cretaceous La Luna Formation of the western Maracaibo Basin, Venezuela. Geological Society of America Special Papers 332, 203–230. doi:10.1130/0-8137-2332-9.203

Dortangs, R.W., Schulp, A.S., Mulder, E.W.A., Jagt, J.W.M., Peeters, H.H.G., Graaf, D.T. de, 2002. A large new mosasaur from the Upper Cretaceous of The Netherlands. Netherlands Journal of Geosciences 81, 1–8. doi:10.1017/S0016774600020515

Dot, J.A.M., Baamonde, J.M., Reyes, D., Whilchy, R., Dot, J.A.M., Baamonde, J.M., Reyes, D., Whilchy, R., 2015. The Cogollo Group and the oceanic anoxic events 1a and 1b, Maracaibo basin, Venezuela. Brazilian Journal of Geology 45, 41–61. doi:10.1590/2317-4889201530192

Dunkle, D.H., 1951. New Western Hemisphere occurrences of fossil selachians. Journal of the Washington Academy of Sciences 41, 344–347.

Erlich, R.N., Macsotay I., O., Nederbragt, A.J., Antonieta Lorente, M., 2000. Birth and death of the Late Cretaceous “La Luna Sea”, and origin of the Tres Esquinas phosphorites. Journal of South American Earth Sciences 13, 21–45. doi:10.1016/S0895-9811(00)00016-X

Erlich, R.N., Macsotay I, O., Nederbragt, A.J., Lorente, M.A., 1999. Palaeoecology, palaeogeography and depositional environments of Upper Cretaceous rocks of western Venezuela. Palaeogeography, Palaeoclimatology, Palaeoecology 153, 203–238. doi:10.1016/S0031-0182(99)00072-3

Everhart, M.J., 2005. Earliest Record of the Genus *Tylosaurus* (Squamata; Mosasauridae) from the Fort Hays Limestone (Lower Coniacian) of Western Kansas. Transactions of the Kansas Academy of Science (1903-) 108, 149–155.

Glikman, L.S., 1980. Evolution of Cretaceous and Cenozoic lamnoid sharks. Akademii Nauk SSSR, Moskova 247 pp. [In Russian].

Glikman, L.S., 1964. Sharks of Paleogene and their stratigraphic significance. Nauka Press 229 Moscow. [in Russian].

Glikman, L.S., 1958. Rates of evolution in lamnoid sharks. Doklady Akademii Nauk Soyuza Sovetskikh Sotsialisticheskikh Respublik 123, 568–571.

Glikman, L.S., 1957. On the systematic significance of accessory denticles in the teeth of sharks of the families Lamnidae and Scapanorhynchidae [in Russian]. Trudy Geologischeskogo Muzeja “A. P. Karpinskogo”, Akademia Nauk SSSR 1, 103–109.

Glikman, L.S., Shvazhaite, R.A., 1971. Sharks of the family Anacoracidae from the Cenomanian and Turonian of Lithuania, Volga region and Middle Asia. Paleontologiya i Stratigrafiya Pribaltiki Belorussii 3, 185–194 [In Russian].

González de Juana, C., Iturralde de Arocena, J., Picard, X., 1980. Geología de Venezuela y de sus cuencas petrolíferas, Foninves. ed. Caracas.

Guinot, G., Adnet, S., Cappetta, H., 2012. An analytical approach for estimating fossil record and diversification events in sharks, skates and rays. PloS ONE 7, e44632. doi:10.1371/journal.pone.0044632

Guinot, G., Cavin, L., 2016. “Fish” (Actinopterygii and Elasmobranchii) diversification patterns through deep time. Biol Rev 91, 950–981. doi:10.1111/brv.12203

Guinot, G., Underwood, C.J., Cappetta, H., Ward, D.J., 2013. Sharks (Elasmobranchii: Euselachii) from the Late Cretaceous of France and the UK. Journal of Systematic Palaeontology 11, 598–671. doi:10.1080/14772019.2013.767286

Hamm, S.A., 2009. New Data on the Occurrence and Distribution of *Ptychodus* from the Upper Cretaceous (Coniacian-Santonian) of Texas. Dallas Paleontological Society, Occasional Papers 8, 1–31.

Hay, O.P., 1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bulletin, United States Geological Survey 179, 1–868.

Huxley, T.H., 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. Proceedings of the Zoological Society of London 1880, 649–662.

Jaillard, E., 1997. Sintesis estratigrafica y sedimentologica del cretaceo y paleogeno de la cuenca oriental del Ecuador.

Juana, C.G. de, Arozena, J.M.I. de, Cadillat, X.P., 1980. Geología de Venezuela y de sus cuencas petrolíferas. Foninves.

Kriwet, J., 2006. Biology and dental morphology of *Priscusurus adruptodontus*, gen. et sp. nov. (Chondrychthyes, Lamniformes) from the Albian (Early Cretaceous) of Peru. Journal of Vertebrate Palaeontology 26, 538–543.

Landemaine, O., 1991. Sélaciens nouveaux du Crétacé supérieur du sud-ouest de la France. Quelques apports à la systématique des élasmobranches. Société Amicale des Géologues Amateurs 1, 1–45.

Leidy, J., 1870. Remarks on ichthyodorulites and on certain fossil mammalians. Proceedings of the American Philosophical Society 22, 12–13.

Lewy, Z., Cappetta, H., 1989. Senonian elasmobranch teeth from Israel. Biostratigraphic and paleoenvironmental implications. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1989, 212–222.

Macellari, C.E., De Vries, T.J., 1987. Late Cretaceous upwelling and anoxic sedimentation in northwestern South America. Palaeogeography, Palaeoclimatology, Palaeoecology 59, 279–292. doi:10.1016/0031-0182(87)90086-1

Méndez, C.E., 1981. La Formación La Luna. Característica de una cuenca anóxica en una plataforma de aguas someras. Proceedings of the 7th Congreso Geológico Venezolano 852–866.

Meyer, R.L., 1974. Late Cretaceous elasmobranchs from the Mississippi east Texas embayments of the Gulf Coastal Plain (Unpubl.). Southern Methodist University, Arlington, Texas.

Moody, J.M., Maisey, J.G., 1994. New Cretaceous Marine Vertebrate Assemblages from North-Western Venezuela and Their Significance. Journal of Vertebrate Paleontology 14, 1–8.

Müller, J.K., Henle, F.G.J., 1838. Systematische Beschreibung der Plagiostomen. Berlin: Veit and Co, 200 pp.

Mutter, R.J., Iturralde-Vinent, M., Carmona, J.F., 2005. The first Mesozoic Caribbean shark is from the Turonian of Cuba: *Ptychodus cyclodontis* sp. nov. (?Neoselachii). Journal of Vertebrate Paleontology 25, 976–978. doi:10.1671/0272-4634(2005)025[0976:TFMCSI]2.0.CO;2

Parámo Fonseca, M.E., 1997. Les vertébrés marins du turonien de la vallée supérieure du Magdalena, Colombie - systématique, paléoécologie, paléobiogéographie. Université de Poitiers.

Pereira, A.A., Medeiros, M.A., 2008. A new sclerorhynchiform (Elsamobranchii) from the middle Cretaceous of Brazil. Rev. Bras. Paleontol. 11, 207–212.

Rafinesque, C.S., 1810. Caratteri di alcuni nuovi generi e nuove specie di animali e pinate della Sicilia, con varie osservazioni sopra i medisimi 3–69.

Rebouças, J.C., Silva Santos, R., 1956. Fauna ictiológica do fosfato de Pernambuco, Brasil. Boletim da Divisão de Geologia e Mineralogia, siver 162, 1–29.

Rees, J., 2005. Neoselachian shark and ray teeth from the Valanginian, Lower Cretaceous, of Wawal, central Poland. Palaeontology 48, 209–221.

Reinhart, R.H., 1951. A new shark of the family Ptychodontidae from South America. University of California Publications in Geological Sciences 28, 195–202.

Renz, O., 1982. The Cretaceous ammonites of Venezuela. Birkhäuser Verlag, Basel.

Renz, O., 1968. Über die Untergattungen *Venezoliceras* Spath und *Laraiceras* n. subgen, der Gattung *Oxytropidoceras* Stieler (Ammonoidea) aus den venezolanischen Anden. Eclogae Geologicae Helvetiae 61, 615–655.

Renz, O., 1959. Estratigrafía del Cretáceo en Venezuela occidental. Boletín de Geología 5, 3–48.

Reuss, A.E., 1845. Die Versteinerungen der Böhmischen Kreideformation. Abtheilung 1: 58 pp. Stuttgart (Schweizerbart).

Schwimmer, D.R., Stewart, J.D., Dent Williams, G., 1997. Scavenging by sharks of the genus *Squalicorax* in the Late Cretaceous of North America. Palaios 12, 71–83.

Shimada, K., 2008. New anacoracid shark from Upper Cretaceous Niobrara chalk of Western Kansas, U.S.A. Journal of Vertebrate Paleontology 28, 1189–1194.

Shimada, K., 1997a. Dentition of the Late Cretaceous Lamniform Shark, *Cretoxyrhina mantelli*, from the Niobrara Chalk of Kansas. Journal of Vertebrate Paleontology 17, 269–279.

Shimada, K., 1997b. Paleoecological relationships of the Late Cretaceous Lamniform shark, *Cretoxyrhina mantelli* (AGASSIZ). J. Paleontol. 71, 926–933.

Shimada, K., Martin, D.J., 2008. Fossil fishes from the basal Greenhorn Limestone (Upper Cretaceous, Late Cenomanian) in Russel County, Kansas, in: Farley, G.H., Choate, J.R. (Eds.), Unlocking the Unknown: Papers Honoring Dr. Richard J. Zakrzewski. Fort Hays Studies, Hays, Kansas, pp. 89–103.

Shimada, K., Schumacher, B.A., Parkin, J.A., Palermo, J.M., 2006. Fossil marine vertebrates from the lowermost Greenhorn Limestone (Upper Cretaceous: Middle Cenomanian) in southeastern Colorado. Journal of Paleontology Memoir 63, 1–45.

Shimada, K., Tsuihiji, T., Sato, T., Hasegawa, Y., 2010. A remarkable case of shark-bitten elasmosaurid plesiosaur. Journal of Vertebrate Paleontology 30, 592–597.

Silva Santos, R., 1968. A paleoictiofauna da formação Santana - Euselachii. Anais da Academia brasileira de Ciências 4, 491–497.

Siverson, M., 1999. A new large lamniform shark from the uppermost Gearle Siltstone (Cenomanian, Late cretaceous) of Western Australia. Transactions of the Royal Society of Edinburgh: Earth Sciences 90, 49–66.

Siverson, M., 1997. Sharks from the Mid-Cretaceous Gearle siltstone, Southern Carnavaron Basin, Western Australia. Journal of Vertebrate Paleontology 17, 453–465.

Siverson, M., 1996. Lamniform sharks of the mid Cretaceous Alinga Formation and Beedagong claystone, Western Australia. Palaeontology 39, 813–849.

Siverson, M., Lindgren, J., Kelley, L.S., 2007. Anacoracid sharks from the Albian (Lower Cretaceous) Pawpaw shale of Texas. Palaeontology 50, 939–950.

Siversson, M., Lindgren, J., Newbrey, M.G., Cederström, P., Cook, T.D., 2015. Cenomanian-Campanian (Late Cretaceous) mid-palaeolatitude sharks of *Cretalamna appendiculata* type. Acta Palaeontologica Polonica 60, 339–384. doi:10.4202/app.2012.0137

Strganac, C., Jacobs, L. l., Polcyn, M. j., Mateus, O., Myers, T. s., Salminen, J., May, S. r., Araújo, R., Ferguson, K. m., Gonçalves, A.O., Morais, M.L., Schulp, A. s., da Silva Tavares, T., 2015. Geological setting and paleoecology of the Upper Cretaceous Bench 19 Marine Vertebrate Bonebed at Bentiaba, Angola. Netherlands Journal of Geosciences 94, 121–136. doi:10.1017/njg.2014.32

Stromer, E., 1927. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharije-Stufe (Unterstes Cenoman). 9. Die Plagiostomen mit einem

Anhang über Käno- und mesozoische Rückenflossenstacheln von Elasmobranchiern. Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Math.-naturwiss. Abt., N.F. 31, 1–64.

Tribovillard, N.-P., Stephan, J.-F., Manivit, H., Reyre, Y., Cotillon, P., Jautée, E., 1991. Cretaceous black shales of Venezuelan Andes: preliminary results on stratigraphy and paleoenvironmental interpretations. Palaeogeography, Palaeoclimatology, Palaeoecology 81, 313–321. doi:10.1016/0031-0182(91)90152-H

Underwood, C., Ward, D., Guinot, G., 2016. Development of understanding of the Mesozoic and Cenozoic chondrichthyan fossil record. Geological Society, London, Special Publications 430, 155–164. doi:10.1144/SP430.4

Underwood, C.J., 2006. Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. Paleobiology 32, 215–235.

Underwood, C.J., Cumbaa, S.L., 2010. Chondrichthyans from a Cenomanian (Late Cretaceous) bonebed, Saskatchewan, Canada. Palaeontology 53, 903–944.

Underwood, C.J., Goswami, A., Prasad, G.V.R., Verma, O., Flynn, J.J., 2011. Marine vertebrates from the middle Cretaceous (early Cenomanian) of South India. Journal of Vertebrate Paleontology 31, 539–552.

Vullo, R., 2015. Les poissons, in: Morel, N. (Ed.), Stratotype Cénomanien. pp. 237–244.

Vullo, R., Cappetta, H., Neraudeau, D., 2007. New sharks and rays from the Cenomanian and Turonian of Charentes, France. Acta Palaeontol. Pol. 52, 99–116.

Vullo, R., Guinot, G., Barbe, G., 2016. The first articulated specimen of the Cretaceous mackerel shark *Haimirichia amonensis* gen. nov. (Haimirichiidae fam. nov.) reveals a novel ecomorphological adaptation within the Lamniformes (Elasmobranchii). Journal of Systematic Palaeontology 14, 1003–1024. doi:10.1080/14772019.2015.1137983

Wanner, J., 1902. I. Die Fauna der obersten weissen Kreide der libyschen Wüste. Palaeontographica 30, 91–152.

Weigmann, S., 2016. Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. J Fish Biol 88, 837–1037. doi:10.1111/jfb.12874

Welton, B.J., Farish, R.F., 1993. The Collector's Guide to Fossil Sharks and Rays from the Cretaceous of Texas. Before Time, Lewisville, Texas, 204 p.

Werner, C., 1989. Die Elasmobranchier-Fauna des Gebel Dist Member der Bahariya Formation (Obercenoman) der Oase Bahariya, Ägypten. Palaeo Ichthyologica 5, 5–112.

Whitley, G.P., 1939. Taxonomic notes on sharks and rays. Australian Zoologist 9, 227–262.

Williston, S.W., 1900. Cretaceous fishes. Selachians and Pycnodonts. University Geological Survey of Kansas 6, 237–256.

Zapata, E., Padron, V., Madrid, I., Kertznus, V., Truskowski, I., Lorente, M.A., 2003. Biostratigraphic, Sedimentologic, and Chemostratigraphic Study of the La Luna Formation (Late Turonian–Campanian) in the San Miguel and Las Hernández Sections, Western Venezuela. PALAIOS 18, 367–377. doi:10.1669/0883-1351(2003)018<0367:BSACSO>2.0.CO;2

Zhelezko, V.I., 1990. Pisces (Selachii). Upper Cretaceous deposits of southern post-Urals (region of the upper Tobol River. Uralian Branch of the Academy of Sciences of USSR, Sverdlovsk 122–133.

Zumberge, J.E., 1984. Source Rocks of the La Luna Formation (Upper Cretaceous) in the Middle Magdalena Valley, Colombia 30, 127–133.

Figure Captions

Figure 1. Location map of the Cementos Andinos and La Luna quarries, Venezuela.

Figure 2. Cretaceous lithostratigraphic units and stratigraphic sections of La Luna and Cementos Andinos quarries. The Sierra de Perijá section is based on Renz (1982) and Erlich et al. (1999). The

fossiliferous horizon in La Luna Quarry is based on Moody and Maisey (1994, p. 2). The Chejendé region section in based on Renz (1959) and González de Juana et al. (1980). Stratigraphic section of the Aguada Member in the Cementos Andinos quarry is modified after Albino et al. (2016).

Figure 3. **A-B,** *Nanocorax* sp., anterolateral tooth (AMU-CURS-906) in **A,** lingual and **B,** labial views. **C-H,** *Squalicorax moodyi* sp. nov. **C-D,** anterior tooth (MBLUZ P-430) in **C,** lingual and **D,** labial views. **E-F,** lateral tooth (MBLUZ P-432-C) in **E,** lingual and **F,** labial views, **holotype**. **G-H,** anterolateral tooth (MBLUZ P-432-D) in **G,** lingual and **H,** labial views. All scale bars equal 2 mm.

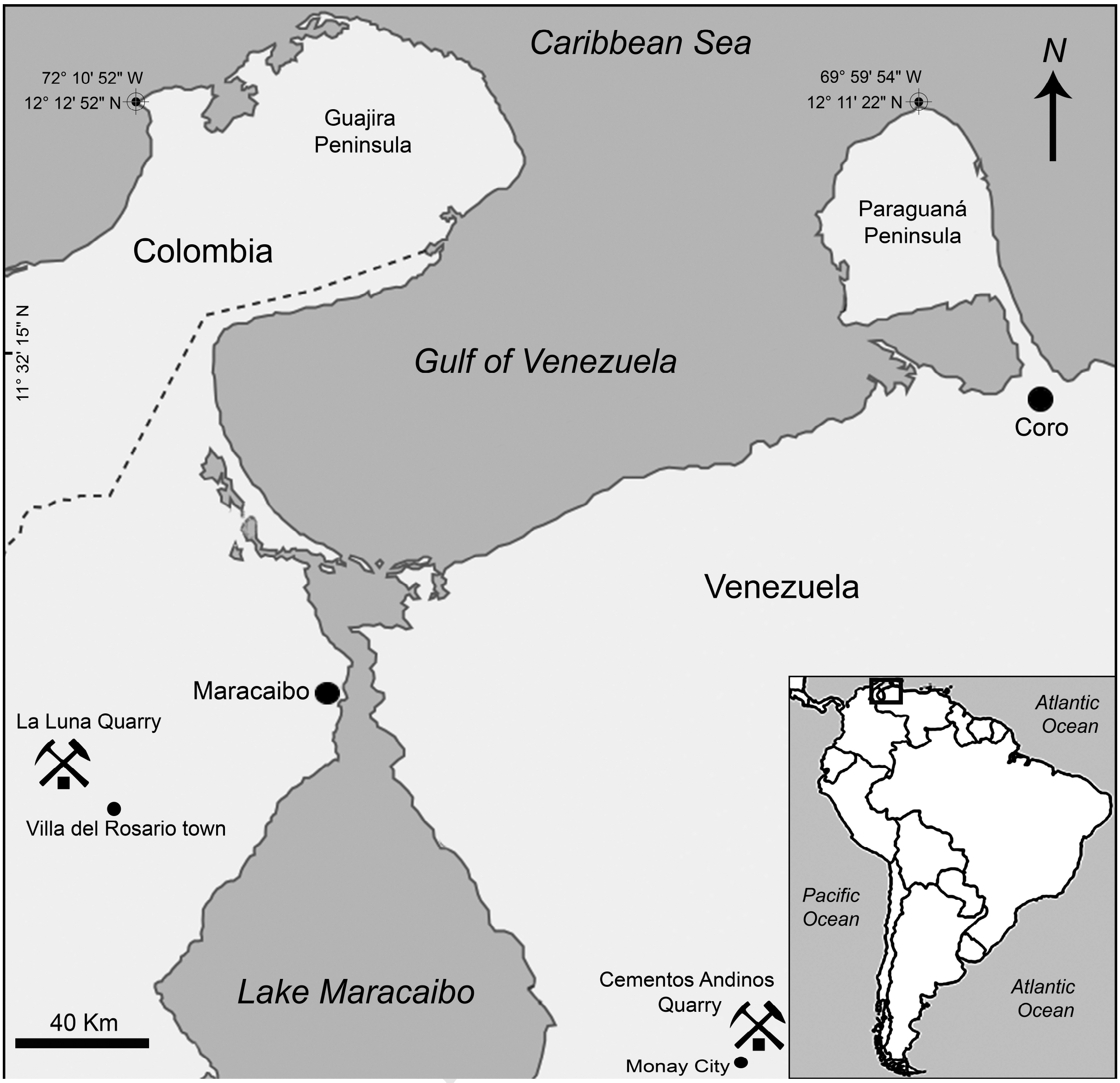
Figure 4. **A-S,** *Squalicorax lalunaensis* sp. nov. **A-B,** anterior tooth (AMU-CURS-894) in **A,** lingual and **B,** labial views. **C-D,** anterolateral tooth (AMU-CURS-895) in **C,** lingual and **D,** labial views. **E-F,** anterolateral tooth (AMU-CURS-896) in **E,** lingual and **F,** labial views. **G-H,** lateral tooth (AMU-CURS-897) in **G,** lingual and **H,** labial views, **holotype**. **I-J,** anterolateral tooth (AMU-CURS-898) in **I,** lingual and **J,** labial views. **K-L,** lateral tooth (AMU-CURS-899) in **K,** lingual and **L,** labial views. **M-N,** lateroposterior tooth (AMU-CURS-900) in **M,** lingual and **N,** labial views. **O-P,** lateroposterior tooth (AMU-CURS-901) in **O,** lingual and **P,** labial views. **Q-R,** posterior tooth (AMU-CURS-902) in **Q,** lingual view, **R,** labial view and **S,** close-up on the labial ornament. All scale bar equal 2 mm except S (1 mm).

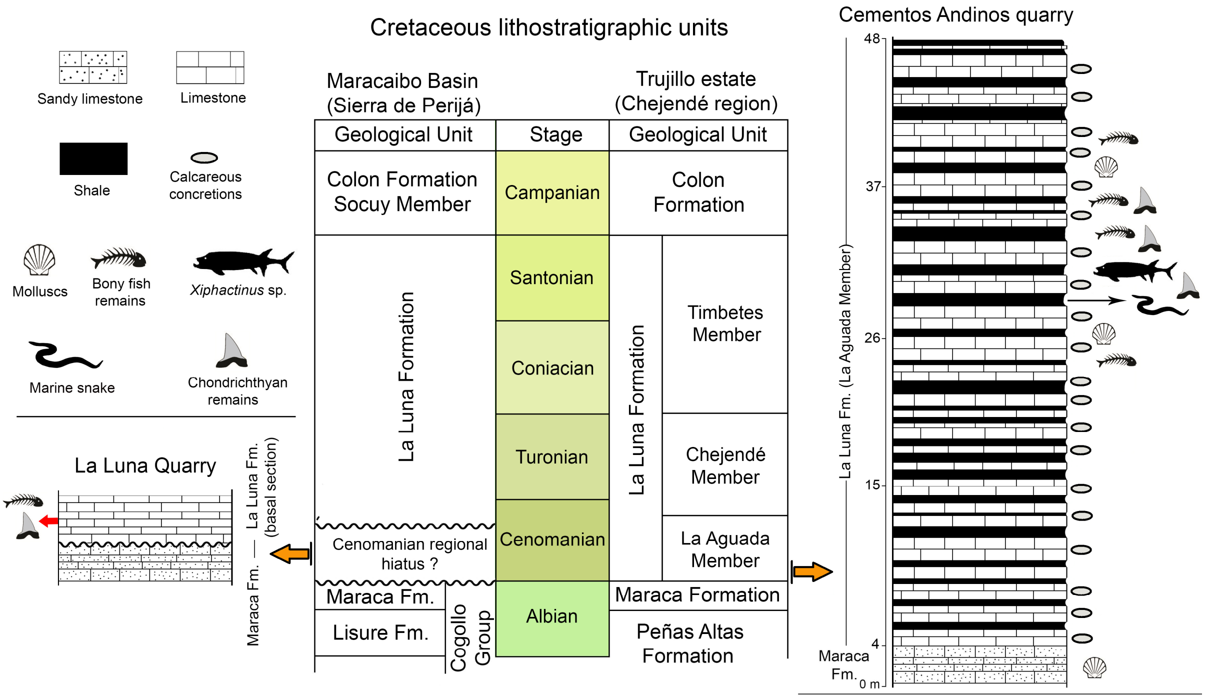
Figure 5. **A-B,** *Squalicorax* aff. *lalunaensis* sp. nov., lateral tooth (AMU-CURS-907) in **A,** lingual and **B,** labial views. **C-I,** *Squalicorax* sp. 1. **C-D,** anterior tooth (MBLUZ P-430-B) in **C,** lingual and **D,** labial views. **E-G,** lateroposterior tooth (MBLUZ P-430-C) in **E,** lingual view, **F,** close-up on the labial foramina and **G,** labial view. **H-I,** lateral tooth (MBLUZ P-15) in **H,** labial and **I,** lingual views. **J-N,** *Squalicorax* sp. 2. **J-K,** lateroposterior tooth (AMU-CURS-892) in **J,** labial and **K,** lingual views. **L-N,** lateral tooth (AMU-CURS-893) in **L,** lingual, **M**, close-up on serrations of the median area of the

mesial cutting edge of main cusp in labial view and **N,** labial views. **O-S,** *Squalicorax* sp. 3. **O-P**, anterior tooth (MBLUZ P-881) in **O,** lingual and **P,** labial views. **Q-S,** lateral tooth (MBLUZ P-430-D) in **Q,** lingual view, **R,** labial view and **S,** close-up on the labial foramina. **T-V,** *Squalicorax* sp. 4, lateral tooth (MBLUZ P-432-B) in **T,** lingual and **U,** labial views and **V**, close-up on serrations of the median area of the mesial cutting edge of main cusp in labial view. All scale bars equal 2 mm except F, M and V (1 mm), and R (500 μm).

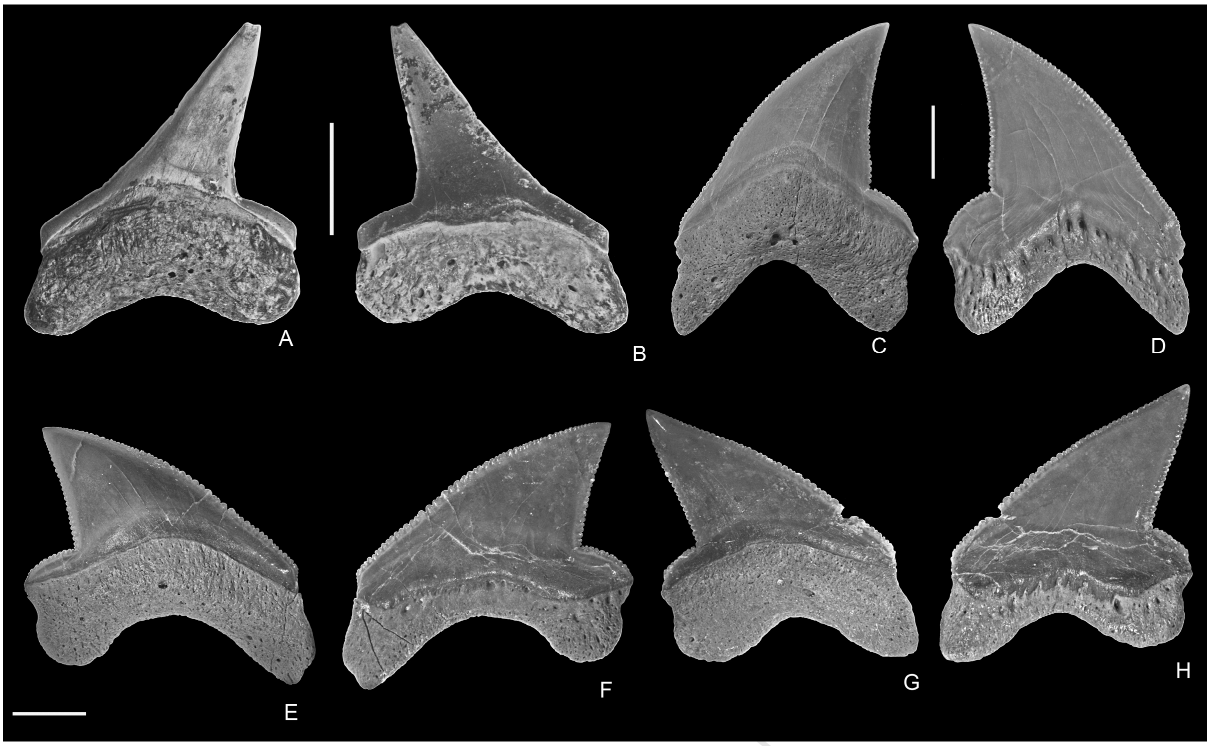
Figure 6. **A-B,** *Cretoxyrhina mantelli*, lateral tooth (MBLUZ P-41) in **A,** lingual and **B,** labial views. **C-O,** *Microcarcharias saskatchewanensis*. **C-D,** anterolateral tooth (MBLUZ P-14) in **C,** lingual and **D,** labial views. **E-H,** anterior tooth (AMU-CURS-890) in **E,** lingual, **F,** labial, **G,** profile and **H,** labial views. **I-L,** anterior tooth (AMU-CURS-891) in **I,** lingual, **J,** labial, **K,** profile and **L,** labial views. **M-O,** lateral tooth (MBLUZ P-14-B) in **M,** lingual, **N,** labial and **O,** labial views. **P,** *Cretolamna* sp., lateral tooth (MBLUZ P-86) in labial view. All scale bars equal 1 mm except A-B (5 mm) and P (2 mm).

Figure 7. **A-M,** *Acutalamna karsteni* gen. et sp. nov. **A-C,** anterior tooth (AMU-CURS-908) in **A,** lingual, **B,** profile and **C,** labial views, **holotype**. **D-E,** anterolateral tooth (AMU-CURS-909) in **D,** lingual and **E,** labial views. **F-J,** lateral tooth (AMU-CURS-910) in **F,** lingual, **G,** basal, **H,** labial/occlusal, **I,** profile and **J,** labial views. **K-L,** anterolateral tooth (AMU-CURS-911) in **K,** lingual and **L,** labial views. **M**, anterior tooth (MBLUZ P-431) embedded in sediment, in lingual view. All scale bars equal 2 mm.


Caribbean Sea
N
72° 10' 52" W
12° 12' 52" N
69° 59' 54" W
12° 11' 22" N
Guajira Peninsula
Paraguaná Peninsula
Colombia
11° 32' 15" N
Gulf of Venezuela
Coro
Venezuela
Maracaibo
La Luna Quarry
Villa del Rosario town
Lake Maracaibo
40 Km
Cementos Andinos Quarry
Monay City
Atlantic Ocean
Pacific Ocean
Atlantic Ocean



Cretaceous lithostratigraphic units
Sandy limestone
Limestone
Shale
Calcareous concretions
Molluscs
Bony fish remains
Xiphactinus sp.
Marine snake
Chondrichthyan remains
La Luna Quarry
La Luna Fm. (basal section)
Maraca Fm.
Maracaibo Basin (Sierra de Perijá)
Trujillo estate (Chejendé region)
Geological Unit
Stage
Geological Unit
Colon Formation Socuy Member
Campanian
Colon Formation
La Luna Formation
Santonian
Coniacian
Turonian
Cenomanian
Albian
Timbetes Member
Chejendé Member
La Aguada Member
Cenomanian regional hiatus ?
Maraca Fm.
Lisure Fm.
Cogollo Group
Maraca Formation
Peñas Altas Formation
Cementos Andinos quarry
48
37
26
15
4
0 m
La Luna Fm. (La Aguada Member)
Maraca Fm.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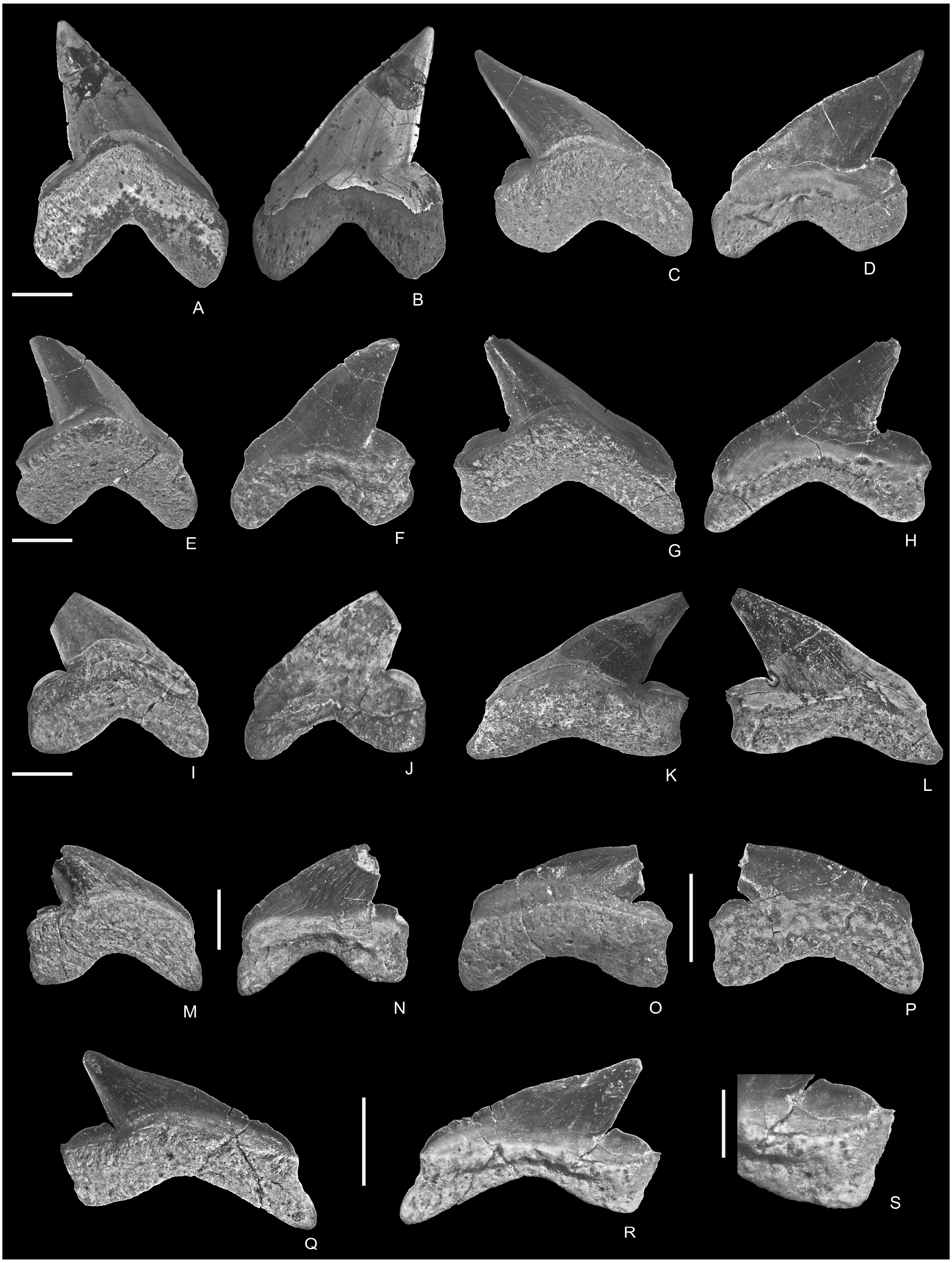
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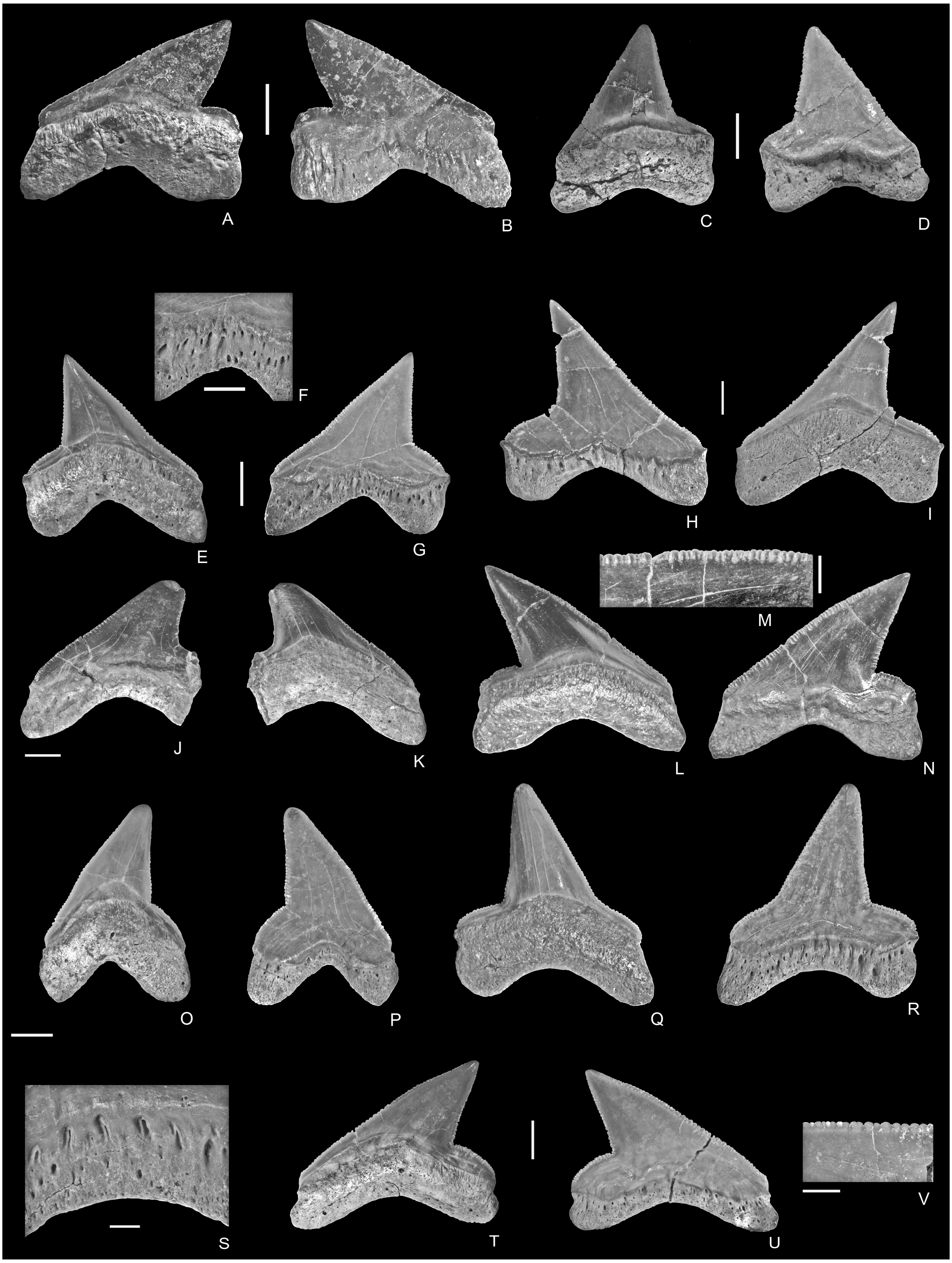
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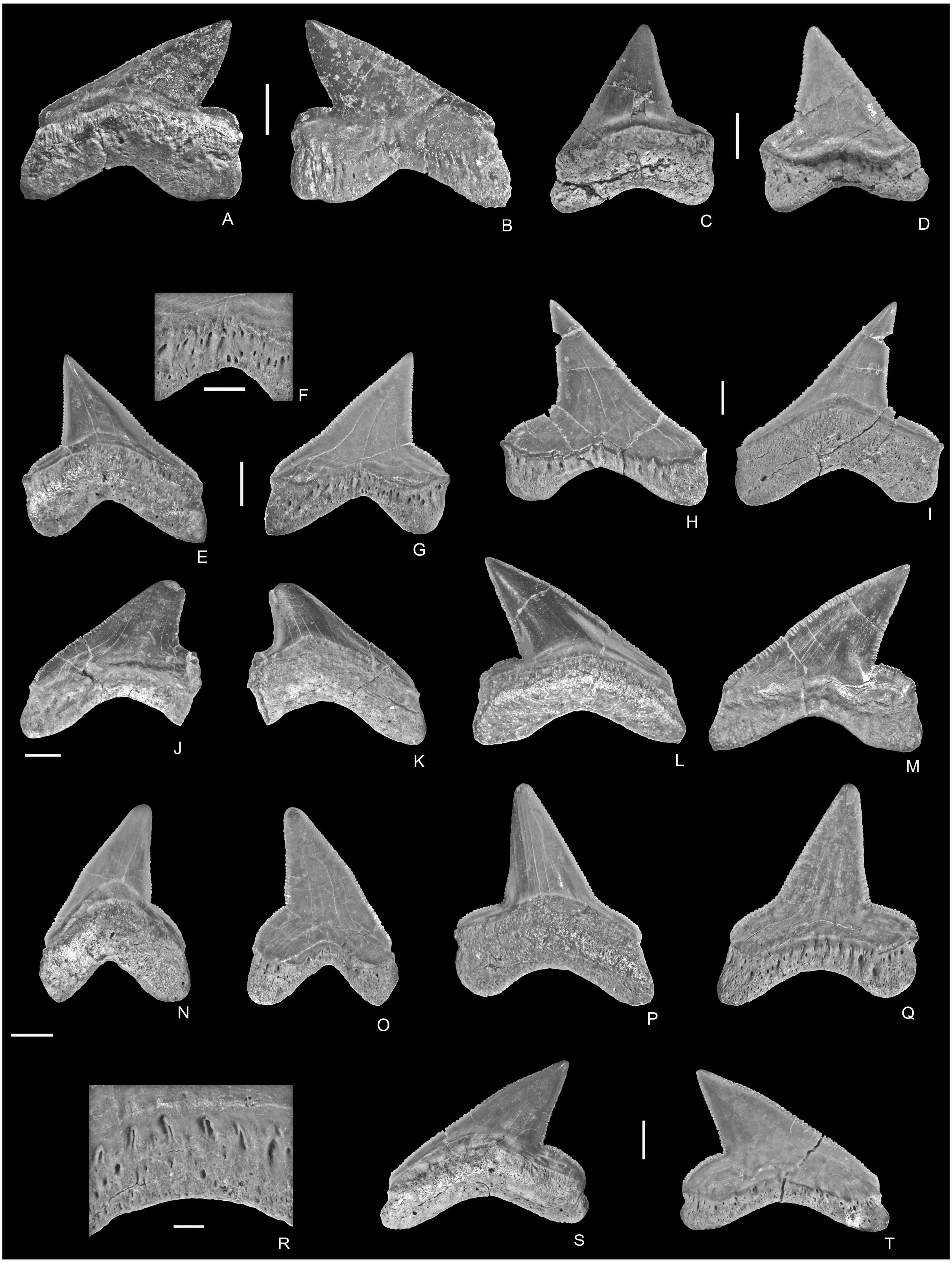
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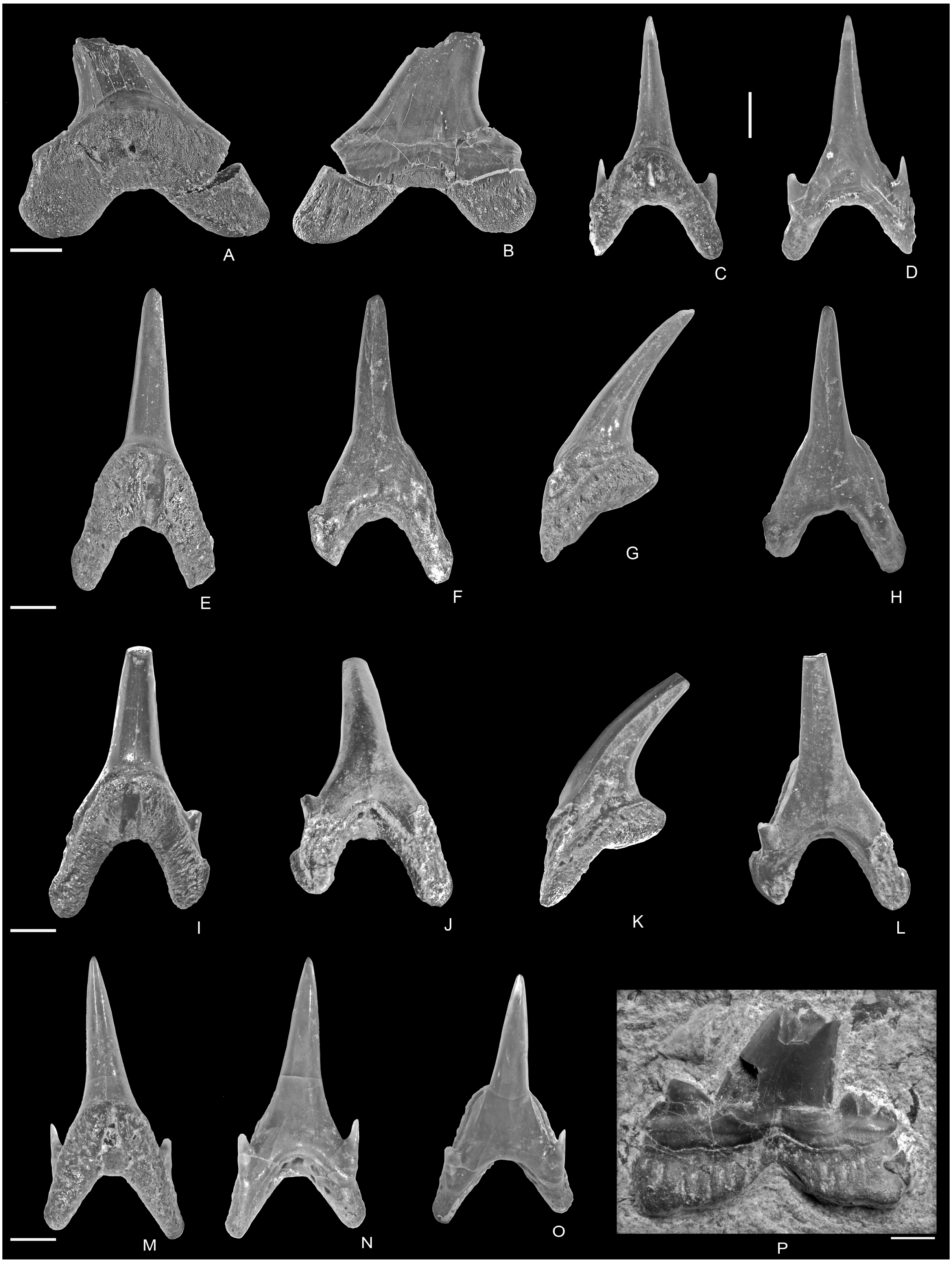

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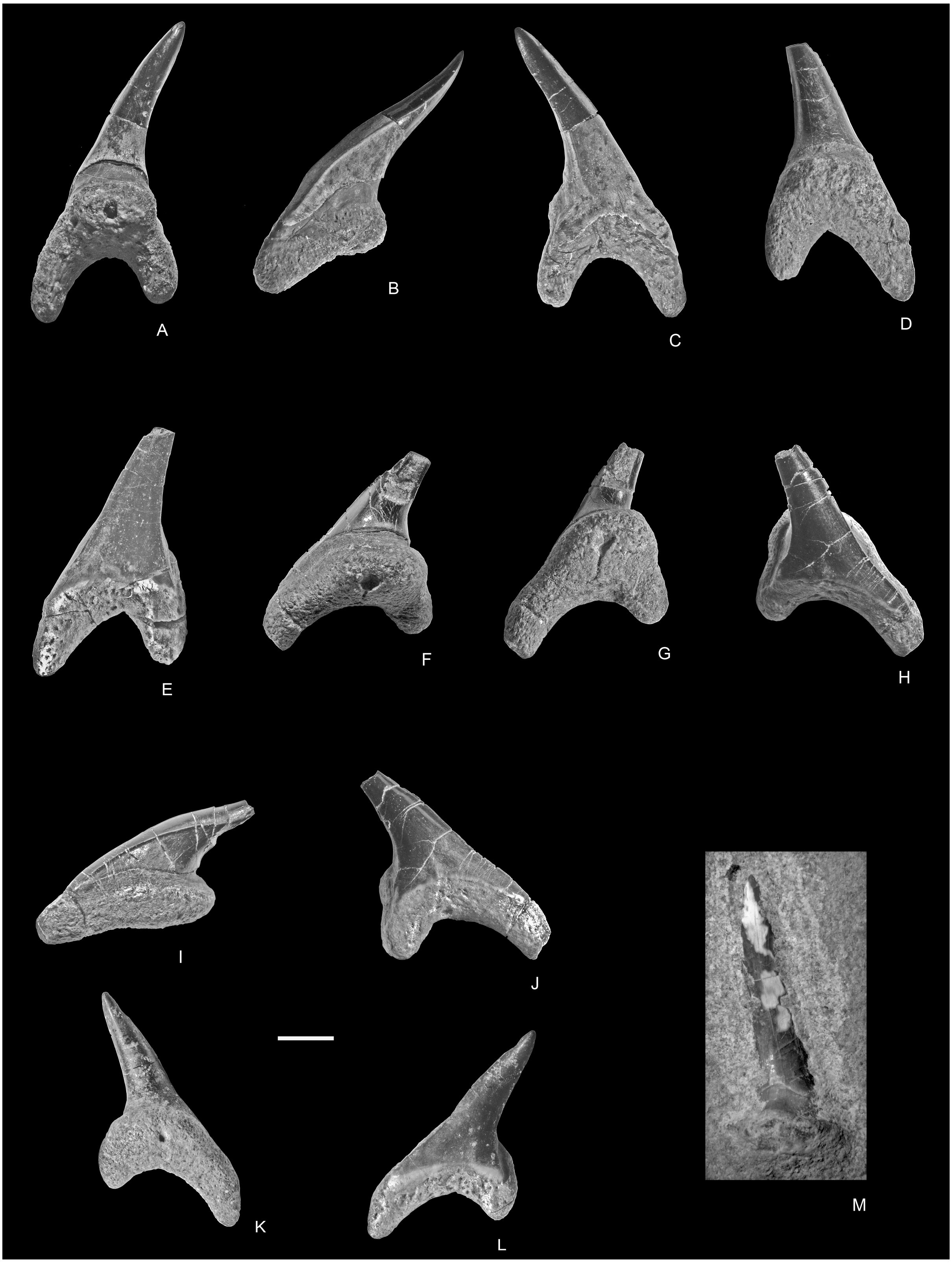
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